Habitat ecology and long-term development of the macrophyte vegetation of north-west German streams and rivers since the 1950s

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„Krickerode war rechtskräftig verurteilt worden. Das Erkenntnis untersagt der großen Provinzfabrik bei hundert Mark Strafe für jeden Kalendertag, das Mühlwasser von Pfisters Mühle durch ihre Abwässer zu verunreinigen und dadurch einen das Maß des Erträglichen übersteigenden übeln Geruch in der Turbinenstube und den sonstigen Hausräumen zu erzeugen, sowie das Mühlenwerk mit einer den Betrieb hindernden, schleimigen, schlingpflanzenartigen Masse in gewissen Monaten des Jahres zu überziehen.“

(Wilhelm Raabe in „Pfisters Mühle“, 1884)

Summary

This PhD thesis deals with the habitat characterization and the long-term development over 60 years of the macrophyte vegetation of north-west German running waters in order to contribute to the knowledge about the ecology of aquatic macrophytes and make use of them as bioindicators. Seventy streams and rivers in the regions Ems-Hunte moraine, Lüneburg Heath, Aller lowlands, northern Harz foothills, base of the Weser-Leine uplands and eastern Holstein were investigated, the emphasis though is on the cross-regional scale. From the analysis of the composition and distribution of the macrophyte communities in relation to river size and physical and chemical water and sediment properties could be concluded that water course depth and current velocity are the most decisive variables for the community composition nowadays, followed by the content of plant-available phosphorus in the sediment. However, it is possible that several decades ago, before the strong intensification of agricultural land-use taking place in the study area since the 1950s, when more pronounced gradients in the nutrient concentrations of running waters existed, chemical variables had a stronger influence on the macrophyte occurrences than today.

By means of a semi-permanent plot approach, the vegetation change between the 1950s and 2010 was investigated, revealing a dramatic decline in species diversity (the overall species pool declined by 27.5 % from 51 to 37 hydrophytic species, plot-level richness by 19.4 % from 4.7 to 3.8 species per relevé), accompanied by a profound shift in community composition from the predominance of potamid species to the predominance of lemnid species. Oligotraphent species such as *Potamogeton gramineus* and *P. polygonifolius* died out in the study sites and the mesotraphent species *Myriophyllum alterniflorum* and *Ranunculus peltatus* declined in their frequency of occurrence by more than 50 %, whereas the eutraphent species *Myriophyllum spicatum* and *Spirodela polyrhiza* increased by more than 100 %. In addition, a change in the species traits leaf longevity and specific leaf area (SLA) was found: in the historical macrophyte communities from the 1950s, evergreen species and species with leaves being thin or rich in air-filled lacunae were abundant, while the recent vegetation from 2010 was characterized by summergreen species with a robust structure (low SLA). On the regional scale, the changes in species composition were most profound in the Ems-Hunte moraine country, where drainage of fens and bogs preceded highly intensive land-use especially since the embankment of the Dümmer lake (1953), and less pronounced in the Lüneburg Heath region, where lowland water courses with a natural structure can still be found.

On the syntaxonomic level, the application of two different phytosociological classification systems revealed deep changes in the macrophyte community structure over six decades. All relevés from vegetated reaches could be assigned to one of the classes

Potamogetonetea, Lemnetea, Phragmitetea or Fontinalietea. While Batrachietalia/Batrachion and Potamogetonetalia/Potamogetonion stands strongly decreased, Nymphaeetalia /Nymphaeion communities gained importance. The observed increase in phytosociologically weakly characterized stands (‘residual communities’) implies losses of highly specialized species. Average similarity was significantly higher in the recent (S_{BC}=0.25) than in the historical (0.22) assemblages, revealing a homogenization of the macrophyte vegetation of north-west German water courses.

The most likely causes of the decline in the macrophyte species and community richness and diversity are accelerated eutrophication processes and river regulation measures, that caused uniformization of the running water habitats in the intensively managed cultural landscape, and regular disturbance. Ongoing efforts to reduce the nutrient loads, as well as the enhancement of the habitat heterogeneity by renaturalizing the structure of the water courses and ecologically compatible weed-cutting techniques and dates are necessary to halt and reverse the diversity decline in the macrophyte vegetation of north-west German streams and rivers. Diverse vegetation stands are an essential element in running water ecosystems, whose functionality is relevant, not least for human welfare.

Zusammenfassung

Diese Arbeit behandelt die Charakterisierung der Habitate und die Langzeit-Entwicklung über sechs Jahrzehnte der Makrophytenvegetation nordwestdeutscher Bäche und Flüsse, um zum Wissen über die Ökologie aquatischer Makrophyten beizutragen und sie als Bioindikatoren zu nutzen. Siebzig Bäche und Flüsse der Regionen Ems-Hunte Geest, Lüneburger Heide, Allerflachland, nördliches Harzvorland, Fuß des Weser-Leine Berglandes und ostholsteinisches Hügelland sind Bestandteil der Studie, wobei der Schwerpunkt auf der überregionalen Betrachtungsebene liegt. Aus der Analyse der Zusammensetzung und Verbreitung der Makrophytengesellschaften im Zusammenhang mit Gewässergröße und physikalischen und chemischen Wasser- und Sedimenteigenschaften schlossen wir, dass Gewässertiefe und Fließgeschwindigkeit von den gemessenen Variablen den größten Einfluss auf die heutige Gesellschaftszusammensetzung haben, gefolgt vom Gehalt pflanzenverfügbaren Phosphors im Sediment. Es ist jedoch nicht auszuschließen, dass vor der im Untersuchungsgebiet seit den 1950ern stattfindenden, starken Intensivierung der landwirtschaftlichen Nutzung, als noch ausgeprägtere Gradienten bei den Nährstoffgehalten der Fließgewässer existiert haben, chemische Größen einen stärkeren Einfluss auf die Makrophytenvorkommen hatten als heute.

Mittels semi-permanenter Dauerflächen haben wir den Vegetationswandel zwischen den 1950ern und 2010 untersucht und einen dramatischen Rückgang der Artenvielfalt festgestellt (der Gesamtartenpool sank um 27.5 % von 51 auf 37 Hydrophytenarten, die Artenzahl pro Aufnahmefläche um 19.4 % von 4.7 auf 3.8 Arten), begleitet von einem umfassenden Bestandsumbau vom Vorherrschen wurzelnder (v.a. potamider) Arten zur Dominanz freischwimmender (v.a. lemnider) Arten. Oligotraphente Arten wie *Potamogeton gramineus* und *P. polygonifolius* sind in den Probeflächen ausgestorben und die mesotraphenten Arten *Myriophyllum alterniflorum* und *Ranunculus peltatus* in ihrer Auftretenshäufigkeit um mehr als 50 % zurückgegangen, während die eutraphenten Arten *Myriophyllum spicatum* und *Spirodela polyrhiza* um mehr als 100 % zugenommen haben. In den Artmerkmalen Blattausdauer und spezifische Blattfläche (SLA) wurden Änderungen festgestellt: In den historischen Makrophytenbeständen der 1950er waren immergrüne Arten und Arten mit dünnen Blättern oder solchen mit viel arenchymatischem Gewebe häufig (große SLA), während die rezenten Bestände von 2010 durch sommergrüne Arten und solche mit robuster Struktur (geringe SLA) gekennzeichnet sind. Die Veränderungen in der Arten-zusammensetzung waren am tiefgreifendsten in der Region Ems-Hunte Geest, wo weitläufige Niedermoore durch Entwässerung insbesondere seit der Eindeichung des Dümmer Sees (1953) intensiv bewirtschaftetem Agrarland gewichen sind, und weniger

ausgeprägt in der Lüneburger Heide, einer der wenigen Tieflandsregionen Deutschlands, in der noch Fließgewässer mit kaum durch den Menschen veränderter Struktur zu finden sind.

Auf der syntaxonomischen Ebene zeigte die Anwendung zweier unterschiedlicher pflanzensoziologischer Klassifikationssysteme tiefe Veränderungen in der Struktur der Makrophytengesellschaften über sechs Jahrzehnte auf. Alle dokumentierten Vegetationsbestände konnten einer der Klassen Potamogetonetea, Lemnetea, Phragmitetea oder Fontinalietea zugeordnet werden. Während Batrachietalia/Batrachion und Potamogetonetalia /Potamogetonion-Bestände stark zurückgegangen sind, haben Nymphaeetalia/Nymphaeion-Gesellschaften zugenommen. Die beobachtete Zunahme pflanzensoziologisch schwach charakterisierter Bestände (Fragmentgesellschaften) deutet auf Verluste bei den hochspezialisierten Arten hin. Im Schnitt waren sich die rezenten Vegetationsbestände signifikant ähnlicher (S_{BC}=0.25) als die historischen (0.22), was eine Homogenisierung der Fließgewässervegetation Nordwestdeutschlands offenbart.

Beschleunigte Eutrophierungsprozesse in den Gewässern und wasserbauliche Maßnahmen in der intensiv genutzten Kulturlandschaft haben zu einer Uniformierung der Fließgewässerhabitate geführt, worin neben häufigen Störereignissen die Hauptursache für die Verluste in Artenreichtum und Vielfalt der Makrophytenvegetation gesehen werden kann. Weitere Anstrengungen zur Reduzierung der Nährstofffrachten, sowie eine Erhöhung der Habitatheterogenität durch strukturverbessernde Renaturierungsmaßnahmen und ökologisch verträgliche Unterhaltungstechniken und -zeitpunkte sind notwendig, um den Diversitätsrückgang in der Makrophytenvegetation nordwestdeutscher Bäche und Flüsse aufzuhalten und umzukehren. Eine artenreiche Vegetation ist ein wichtiger Baustein in Fließgewässer-Ökosystemen, deren Funktionsfähigkeit nicht zuletzt auch für das menschliche Wohlergehen von Bedeutung ist.

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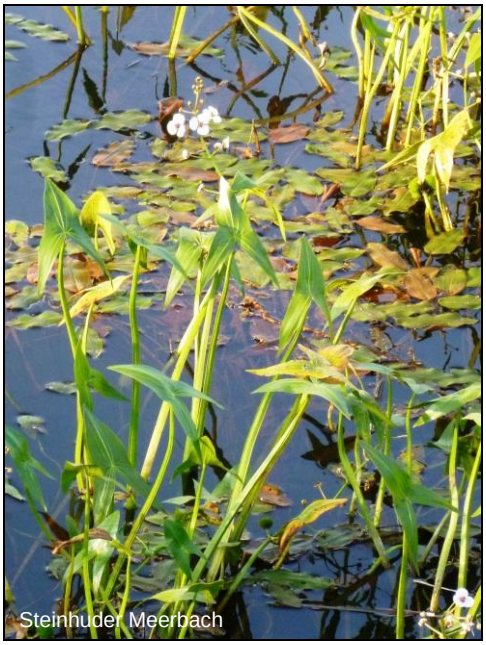
Chapter 1

General introduction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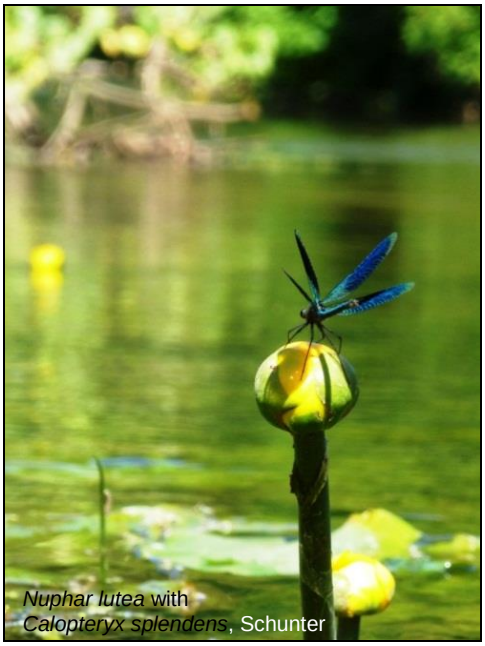
Nuphar lutea with *Calopteryx splendens*, Schunter

Brief history of running water vegetation research

A macrophyte is an "*aquatic photosynthetic organism, large enough to see with the naked eye, growing permanently or periodically submerged below, floating on, or up through the water surface*" (Chambers et al. 2008). The earliest studies on freshwater macrophytes deal for example with aspects of taxonomy, toxicity, life history and leaf anatomy (Pulteney 1800, Palisot de Beauvois 1816, Kützing 1832, Tuckerman 1849, Sauvageau 1891). Limnology [Greek: λίμνη ('limnh') = lake], the scientific study of freshwater ecosystems, is a specialization of ecology with the first textbook by Forel (1901) being available at the beginning of the twentieth century. Since the foundation of the International Society of Limnology (Societas Internationalis Limnologiae) in 1922, running water research is explicitly incorporated in this field (Schwoerbel 1993). The first monographic studies on running water macrophyte vegetation as related to different habitat qualities originate from Central Europe (Tansley 1911, Koch 1926, Butcher 1927, Horvatić 1931, Roll 1939, Steusloff 1939), North America (Muenscher 1931, Thomson 1944, Moyle 1945, Jones 1955) and South Africa (Weintroub 1933), bearing the seeds for the application of aquatic plants as bioindicators. With the inspection of the vegetation of tropical rivers (Lebrun 1947, Cook 1968) also the observed spread of tropical aquatic weeds as for example *Eichhornia crassipes* came into focus (Bard 1965, Bennett 1967). The classification system of aquatic plant taxa into life form (e.g. pleustophytic or rhizophytic) and growth form types (e.g. ceratophyllid, nymphaeid or batrachid) was basically developed by Glück (1924), Luther (1949), Den Hartog & Segal (1964) and Mäkirinta (1978). By now, taxonomical questions in some genera as for example *Potamogeton* (Wiegleb & Kaplan 1998, Preston 1995), *Callitriche* (Schotsmann 1967, Dersch 1987, Lansdown 2006) and *Ranunculus* (Cook 1966, Wiegleb & Herr 1983) still require clarification, possibly by using a genetic approach (Kaplan & Štěpánek 2003, Bradley et al. 2011, Telford et al. 2011).

Evolution and physiological characteristics of aquatic macrophytes

The terrestrial higher plants evolved in the Ordovician period (c. 450 million years ago) from the Characeae being a family of complex structured Chlorophyta (green algae) with a stem and lateral branches (Bresinsky et al. 2008). The evolution of aquatic angiosperms probably emanated from terrestrial angiosperms involving processes of reduction and loss with regard to more complex ancestors (Arber 1920, Les et al. 1997). The adaptation of terrestrial plants to the life in the water is thought to have taken place independently many times, because despite the low proportion of higher plant species being macrophytic (2 %), this group is very heterogeneous, particularly with regard to reproduction strategies and growth forms, hinting at individual evolutionary lines (Philbrick & Les 1996, Cook 1999).

Submerged plants show a variety of adaptations to the life under water: leaves, shoots and rhizomes are typically rich in gas-filled lacunae causing buoyancy and facilitating oxygen and carbon dioxide transport within the plants (Sculthorpe 1967, Sand-Jensen & Prahl 1982). Submerged leaves have only a thin cuticle with a water permeability about three times higher than that of surfaces from emergent leaves (Schönherr 1976), allowing effective nutrient uptake (Sand-Jensen et al. 1992). Early studies attributed anchoring in the sediment as the main function to the roots of hydrophytes (Brown 1913, Sutcliffe 1962), but their roots also play a significant role in nutrient uptake (Denny 1972, Chambers et al. 1989). Defense strategies of macrophytes include the translocation of nutrients and shortening of the growth period as observed for *Potamogeton perfoliatus* under grazing pressure (Miler & Straile 2010). For *Stratiotes aloides* the allelopathic inhibition of algal growth has been observed (Mulderij et al. 2005) and *Elodea nuttallii* is capable of performing chemical defense against herbivorous insects (Erhard et al. 2007).

Aquatic plants except for bryophytes have the ability to use carbon not only from carbon dioxide, of which the uptake is a diffusive process, but also from bicarbonate being actively transported through the cell membrane (Madsen 1993). Depending on the pH of the water, inorganic carbon is predominantly present in the form of carbon dioxide (at 0 °C: pH <6.5), bicarbonate (pH 6.5–10) or carbonate (pH >10) (Gessner 1959). Another specific feature, though only of a few macrophyte species, is the capability to perform Crassulacean acid metabolism (CAM) being a photosynthesis mechanism involving nighttime fixation of carbon in the form of malate acid for decarboxylation at daytime. The CAM occurs in terrestrial plants adapted to aridity and in aquatic plants, like *Isoëtes lacustris* or *Litorella uniflora*, adapted to carbon limitation (Keeley 1998).

Ecological functions of river macrophytes

Macrophytes increase the diversity of ecological niches by providing hiding place, feeding habitat and spawning ground or serving as food for fish (Petr 2000, Valley et al. 2004), invertebrates (Berg 1949, Rooke 1986, Brusven et al. 1990, Newman 1991) and waterfowl (Søndergaard et al.1998). An example for an indirect positive effect of aquatic rhizophytes in running waters for animals depending on the hyporheic interstitial - like the brown trout being the host fish of the freshwater perl mussel - is the reduction of the load of fine particles in the water column. Due to erosion, caused for example by hydraulic engineering or coming from agricultural land, high amounts of suspended matter can regularly be found in lowland rivers, silting the interstitial (Altmüller & Dettmer 1996). As macrophytes reduce the current velocity within the vegetation patches, they cause sedimentation and act as “sand filters” (Sand-Jensen 1998). They also prevent erosion from the banks by fixing the sediment with their roots. Macrophytes contribute to the “self-purification” of water bodies directly by uptake of

nutrients and oxygenation of the water and the sediment, but also indirectly by building the substrate for epiphytic algae that multiply the same effects (Engelhardt & Ritchie 2001, Dhote & Dixit 2009).

Practical applications of aquatic macrophytes

An application of aquatic macrophytes is the use as bioindicators. Although the knowledge about the aut- and synecological tolerance ranges of macrophyte species or communities against specific factors is still insufficient (Lansdown & Bosanquet 2010), the sensitiveness of macrophytes to changes in environmental conditions as for example eutrophication and pollution has been verified by means of field (Kohler et al. 1974, Kutscher 1984, O'Hare et al. 2010) and experimental studies (Grube 1975, Glänzer et al. 1977, Geurts et al. 2009). In the European Water Framework Directive (European Union 2000) macrophytes are used as one of five biological components for the assessment of the ecological quality of water bodies.

Other applications of macrophytes include the use of fast growing macrophytes like *Lemna minor*, *Spirodela polyrhiza* or *Salvinia minima* for phytoremediation purposes like organic wastewater treatment (Bergmann et al. 2000, Körner et al. 2003, Olguín et al. 2007). The gained protein-rich phytomass can be harvested and used as animal food or for the production of fuel ethanol (Culley & Epps 1973, Cheng & Stomp 2009). *Lemna minor* is also frequently used to test chemicals for environmental toxicity in a standard test (International Organization for Standardization 2005).

Threats to the phytodiversity in running waters: eutrophication and alterations of the morphology of water courses

The vegetation of western European streams and rivers, consisting of c. 100 macrophyte species (Haslam 1987), has largely been affected by eutrophication and construction measures during the second half of the twentieth century (Riis & Sand-Jensen 2001, Ellenberg & Leuschner 2010). Eutrophication, the increase in productivity of a water body caused by the addition of nutrients, may be a slow natural process, but occurs as man-made phenomenon especially in industrialized countries due to regular fertilizer or sewage inflow with the surface water (Lampert & Sommer 1993). On German farmland, phosphorus fertilization has dropped after a peak in the 1970s, while the nitrogen input by fertilization is still about four times higher today than in the 1950s (Figure 1.1). The negative effect of eutrophication on macrophytes is mostly an indirect one, in the way that phytoplankton and epiphytic algae get to a mass reproduction shading out submerged, rooted plants (Phillips et al. 1978). In few cases of macrophyte decline, direct ammonium toxicity has been diagnosed (Smolders et al. 1996, Zantout et al. 2011). In Germany, especially in the lowlands, in the

course of melioration the majority of the streams and rivers has considerably been modified in their morphological structure (Umweltbundesamt 2011). Alterations of the morphology of water courses by construction works mostly result in degraded habitats for macrophytes, due to increased water turbidity from erosion and a loss of sheltered inlets, backwaters and transition zones to floodplain areas (Lubke et al. 1984, Baattrup-Pedersen & Riis 1999).

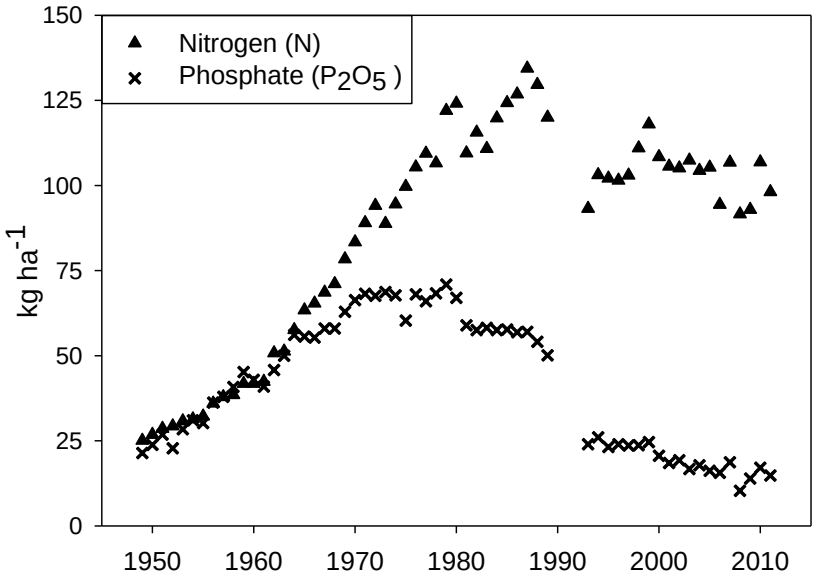

Figure 1.1 Nutrient inputs by fertilization on German farmland between 1949 and 2011, based on data taken from Statistisches Bundesamt (2012)

Thesis aim and chapter outline

At the beginning of this PhD thesis stood the idea that the potential of aquatic plants as long-term indicators for environmental conditions was not yet extendedly explored and applied in Central European running waters. The aim of this study is to draw a multi-faceted picture of the macrophyte vegetation of streams and rivers as related to habitat characteristics and its temporal development over 60 years using the example of the north-west German lowlands.

Chapter 1 presents the background and the concept of the study, giving an overview of the state of knowledge about the vegetation of running waters and information on the natural conditions and anthropogenic influences in the study area.

In **chapter 2** correlations between the environmental conditions of running waters and the macrophyte occurrences recorded in 289 sites in 2010/2011 are presented. Relevant environmental factors (among those measured are pH and nutrient contents of the water and the sediment, river size and flow velocity) being decisive for the current vegetation composition were to be identified testing on the species and community levels.

In **chapter 3** the floristic compositions of 338 vegetation relevés from the 1950s and the same number of relevés from 2010/2011 are compared, asking whether changes in the

species richness and diversity have occurred over the six decades. Species traits like leaf longevity and specific leaf area (SLA) were included in the comparison, as a relation with environmental conditions is assumed, as well as environmental variables like current velocity and the Ellenberg indicator value for nitrogen, to extend the basis for identifying causes of observed changes. For a subset of the data (29.6 % of the study sites) a three-step comparison between the 1950s, the 1980s and 2010 allowed the analysis of the time course of the species richness and diversity development.

For **chapter 4** the macrophyte assemblages from the 1950s and from 2010/2011 were classified in order to detect changes in the macrophyte community structure over the six decades. Assuming that two independent classification systems should lead to more robust conclusions on vegetation change than one system alone, two different phytosociological character species-based systems were applied. Community development was analyzed on the landscape and cross-regional scale, also in relation to the change in habitat characteristics.

In **chapter 5** the synthesis of the three parts of the study as presented in the chapters 2 to 4 is given, combining the knowledge about the habitat preferences of the different macrophyte species and communities and about the floristic and syntaxonomic developments over six decades. Methodological aspects of assessing long-term change in macrophyte communities are pointed out, the probable causes of the vegetation change in running waters are outlined and possible future developments discussed.

The study area: geology, climate and human influence

The federal states Lower Saxony, Schleswig-Holstein and the northern part of North Rhine-Westphalia make up the north-west German lowlands being a morphologically diverse Pleistocene landscape, bordered by the Northern Sea, Denmark and the Baltic Sea in the north, the Netherlands in the west, Mecklenburg-Vorpommern, Brandenburg and Saxony-Anhalt in the east and the Central German highlands in the south. Glacial processes formed the relief until the end of the last (Weichsel) Ice Age 10,000 years ago and since about 1,000 years anthropogenic colonization influences the shape of the landscape surface (Liedtke & Marcinek 2002). Melioration measures improving the agricultural land use are conducted since the Middle Ages. In terms of the Köppen-Geiger climate classification, the north German lowlands belong to the warm, temperate and year-round humid zone (Kottek et al. 2006). The coastal regions (Schleswig-Holstein and the north-western parts of Lower Saxony) are characterized by an Atlantic climate with low temperature amplitudes (c. 1.3 °C in the winter and c. 15.9 °C in the summer, Kiel) and relatively high precipitation amounts (c. 754 mm yr^{-1}, Kiel), whereas the south-eastern parts of the study area (the northern Harz foothills and base of the Weser-Leine uplands) have a continental climate with higher

temperature amplitudes (c. 1.0 °C in the winter and c. 16.6 °C in the summer, Braunschweig) and lower precipitation amounts (c. 656 mm yr^{-1}, Hannover) (means over thirty years, Deutscher Wetterdienst 2013).

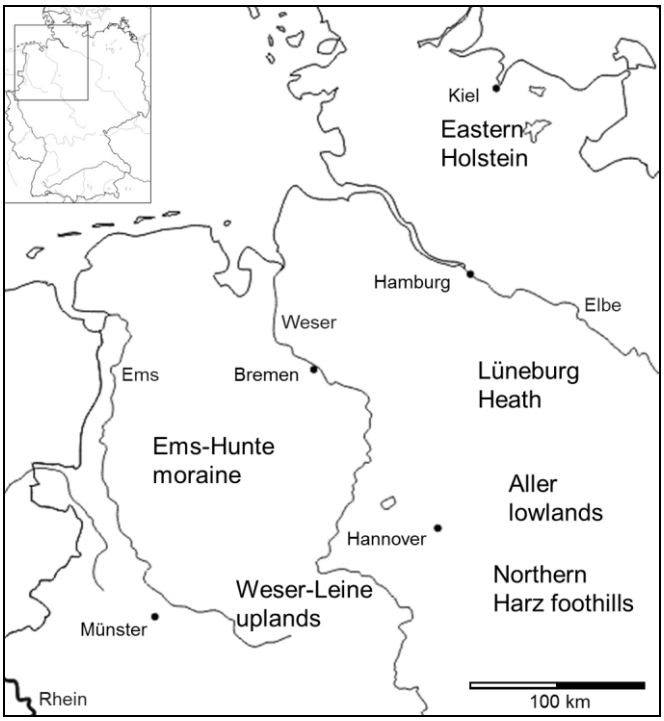

Figure 1.2 Location of the study regions within the north-west German lowlands: the Ems-Hunte moraine country (78 plots), the Lüneburg Heath and Aller lowlands (108 plots), the northern Harz foothills and base of the Weser-Leine uplands (91 plots) and the eastern Holstein moraine country (61 plots)

Table 1.1 Number of studied rivers and semi-permanent plots per study region, mean widths and depths of the studied river reaches in the 1950s and in 2010/2011 (means ± SD) and most intensively sampled rivers

Region	No. of rivers	No. of plots	Reach width 1950s [m]	Reach width 2010/11 [m]	Reach depth 1950s [m]	Reach depth 2010/11 [m]	Most intensively sampled rivers (no. of plots)
Ems-Hunte moraine	21	78	7.7 ±4.4	12.6 ±12.9	0.9 ±0.5	1.4 ±0.7	Hunte (32), Elze (6)
Lüneburg Heath with Aller lowlands	24	108	9.9 ±7.8	9.7 ±7.5	0.8 ±0.5	0.8 ±0.6	Lachte (16), Aller (15), Örtze (15)
Harz foothills with base of Weser-Leine uplands	19	91	9.4 ±7.8	9.6 ±7.4	0.8 ±0.7	0.9 ±0.7	Schunter (29), Oker (27)
Eastern Holstein	6	61	3.9 ±3.3	8.7 ±7.4	0.8 ±0.5	1.2 ±0.6	Kossau (31), Schwentine (12)

Seventy streams and rivers were studied, belonging to the catchments of the Rhine, the Ems, the Weser and the Elbe flowing into the Northern Sea, or draining to the Baltic Sea. They are located in six regions (Figure 1.2). The Ems-Hunte moraine country (15-50 m a.s.l.), located between the rivers Ems and Weser, is characterized by base-poor, sandy and sometimes loamy soils originating from the penultimate (Saale) Ice Age (Meynen & Schmithüsen 1962). Especially in the south around the c. 12 km² big Dümmer lake, rests of fens and bogs are distributed, which had once been dominant in this region before having widely been drained for land cultivation during the last centuries (Finck et al. 1997). Today, an intensive agricultural management predominates. Settlements and forests account for an area below the national average, while the area of agriculturally used land (67-73 %) is above the national average of 55 % and the proportion of this land being used for crop cultivation has risen between the 1950s (34-48 %), when wet meadows used for cattle grazing were still common, and 1991 (63-78 %), due to an improvement of the drainage techniques (Finck et al. 1997).

The Lüneburg Heath (30-60 m a.s.l.), lying between the rivers Elbe and Aller, is characterized by nutrient-poor, acid sand soils (Meynen & Schmithüsen 1962). About 2,000-3,000 BC the first settlers started cutting trees and establishing a heathland agriculture that reached a peak in the eighteenth century with c. 75 % of the Lüneburg Heath area being heathland (Finck et al. 1997). Since then reforesting, mainly with managed pine and spruce forests, occurred that decreased the proportion of heathland to c. 20 % of the area of this region, where intensive crop cultivation also plays a role since the 1950s (Finck et al. 1997). Remarkably, in the Lüneburg Heath structurally unmodified streams and rivers can still be found (Niedersächsisches Landesamt für Ökologie 2001). The Aller lowlands (30-60 m a.s.l.), located between the Lüneburg Heath in the north and the northern Harz foothills in the south, are characterized by base-poor sand soils and alluvial deposits (Meynen & Schmithüsen 1962). Forests are underrepresented in this region, while settlements and agricultural land represent the national average; the predominant land-use type is crop cultivation (Finck et al. 1997). In the chapters 3 and 4, the sites in the Aller lowlands were included in the Lüneburg Heath region, due to resembling bedrock chemistries.

The northern Harz foothills (45-160 m a.s.l.), located in a zone with Pleistocene loess deposits at the base of the Central highlands, are characterized by relatively base- and nutrient-rich sandy or loamy soils (Meynen & Schmithüsen 1962). This region has a long dating back tradition of crop cultivation; forests are mainly restricted to the hill tops and most of the rivers were subject to hydro-engineering and some were also affected by potash salt and coal mining (Finck et al. 1997). The base of the Weser-Leine uplands (90-210 m a.s.l.) is also located in the transition zone between the northern lowlands and the Central highlands, being characterized by base-rich soils (Meynen & Schmithüsen 1962). In the chapters 3 and

4 the sites at the base of the Weser Leine uplands were integrated in the northern Harz foothills region, because in all those sites runoff and groundwater are influenced by the silicate- or carbonate-rich bedrock of the uplands.

The eastern Holstein moraine country (25-40 m a.s.l.), located between the Baltic Sea and the Elbe valley, is characterized by relatively base- and nutrient-rich, sandy or loamy young moraine soils and littered with lakes originating from the Weichsel Ice Age (Meynen & Schmithüsen 1962). The proportion of forested area is low and intensive crop cultivation is the predominant land-use type (Finck et al. 1997).

The streams and rivers have sandy sediments, which are partly overlain by gravel especially in the Lüneburg Heath and northern Harz foothills regions, where summer-cool, rhithral water courses can be found. In the potamal rivers of the Ems-Hunte and eastern Holstein moraine regions, sapropels and organic deposits are not uncommon. Modifications to the hydromorphology of the investigated water courses between the 1950s and 2010/2011 were most pronounced in the Ems-Hunte moraine and eastern Holstein regions, whereas only slight widening and deepening occurred in the Lüneburg Heath and northern Harz foothills regions (Table 1.1).

Nomenclature

The nomenclature of the species follows Buttler & Thieme (2011) for vascular plants and Koperski et al. (2000) for bryophytes. Syntaxonomic vegetation units are named after Preising et al. (1990), Chytrý (2011), or if bryophyte-dominated after Schubert (2008).

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Chapter 2

Relationships between macrophyte vegetation and physical and chemical conditions in north-west German running waters

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(*Aquatic Botany*, in press)

Ranunculus peltatus, Grenzkanal

Kossau

Potamogeton crispus and *P. pectinatus*, Altenau

Determination of the sediment P_{resin} content

Abstract

The macrophyte vegetation of Central Europe's rivers and streams has markedly impoverished during the last decades as a consequence of man's impact on water chemistry and hydromorphology. Here, we examine relationships between species composition and about 35 physical, chemical and river morphological parameters in 69 water courses (291 sampling plots) in the Pleistocene lowlands of north-west Germany for identifying indicator species and environmental parameters suited for categorizing habitat types, growing conditions and the anthropogenic influence in these profoundly altered aquatic ecosystems. Of the 94 species recorded in total, 31 frequent taxa were analyzed for their affinity to specific environmental conditions. Current velocity and water depth (river size) were the most influential determinants of community composition while chemical factors were of secondary importance. We identified eight macrophyte assemblages, each with their own distinctive indicator species and characteristic combinations of growth forms. Small rhithral, relatively nutrient-poor water courses with high velocity were indicated by *Myriophyllum alterniflorum* and *Ranunculus peltatus,* while *Elodea nuttallii, Myriophyllum spicatum* and *Spirodela polyrhiza* characterized large, potamal water courses with high trophy. We conclude that macrophytes may serve as valuable bioindicators of habitat conditions even in anthropogenically altered running waters, but the specific effects of physical, chemical, and river morphological factors are difficult to separate.

Keywords: bioindication, current velocity, macrophyte assemblages, sediment characteristics, water chemistry

Introduction

There is general consensus that the distribution patterns of freshwater macrophytes in flowing waters are largely determined by a few physical and chemical factors including current velocity (Janauer et al. 2010, Grinberga 2011), the grain size and nutrient content of the bottom substrate (Baattrup-Pedersen and Riis 1999, Paal et al. 2007), the trophic state of the water body (Demars and Harper 1998) and the geochemistry of the catchment (Grasmück et al. 1995, Barendregt and Bio 2003, Baattrup-Pedersen et al. 2008). Even though current velocity was identified already eighty years ago as a decisive factor determining the vegetation structures in running waters (Butcher 1933), in the subsequent decades, most Central European studies on the ecology of river macrophyte vegetation focused on hydrochemistry. The principal objective was to establish a macrophyte-based indicator system for water pollution assessment, comparable to the standardized Central European macrozoobenthos-based saprobic system (Grube 1975, Weber 1976, Kohler

1978, Wiegleb 1979, Janauer 1981). These investigations revealed, however, that the influence of physical factors, notably current velocity, seems to overlay the effects of sediment and water chemistry on community composition in many cases, causing a more or less distinct downstream zonation of vegetation. In contrast, chemical factors were found to differentiate only within the vegetation zones defined by the gradient of current velocity (Wiegleb 1984, Bernez et al. 2004, Daniel et al. 2006). Macrophyte indices for the assessment of the trophic status of rivers have been developed in the United Kingdom (MTR = Mean Trophic Rank, Holmes et al. 1999), Germany (TIM = Trophic Index of Macrophytes, Schneider and Melzer 2003) and France (IBMR = Macrophyte Biological Index for Rivers, Haury et al. 2006). Despite regional differences in the list of indicator species, the trans-national validity of macrophyte indices has partly been confirmed (Schneider 2007). Nevertheless, the applicability of these indicators may be limited allowing only very rough assessments of environmental conditions, and the limitations are subject to ongoing discussion (e.g. Demars et al. 2012).

Recently, macrophyte studies in rivers have been triggered by the implementation of the European Water Framework Directive (WFD, European Union 2000) that brought the so-called 'good ecological condition' to the centre of attention. Integrative indicators are needed that are responsive to both physical and chemical factors and give information about the state of river bed morphology and the intensity of anthropogenic pressure. Macrophytes might be good indicator organisms, because in their growth and distribution they respond to all of these factors (Meilinger 2003, Schaumburg 2004, Kuhar et al. 2011). However, pronounced changes in Central Europe's macrophyte vegetation in the last 50 years (Riis and Sand-Jensen 2001, Ellenberg and Leuschner 2010, Steffen et al. 2013) make it necessary to re-evaluate the indicator value of macrophyte species and assemblages. Even though some attempts to differentiate between macrophyte assemblages hinted at the existence of only loose associations (Gessner 1955, Brux et al. 1988), a number of characteristic assemblages can be identified in Central European rivers (e.g. Weber-Oldecop 1969, Herr et al. 1990, Holmes et al. 1998, Paal and Trei 2004). Notwithstanding that the major drivers of vegetation distribution in rivers are largely known, we go a step further and try to assess the relative importance of hydromorphological, physical and chemical factors as possible controls of macrophyte occurrence.

We present the results of a study in 291 plots covering 69 rivers and streams in the north-west German lowlands, which examined the correlation of species presence and community composition with important morphological, physical and chemical properties of the water bodies. We investigated the environmental variables water depth, current velocity, the degree of anthropogenic alteration of river morphology, the pH and nutrient concentrations (N, P, Ca, K, Mg) of the sediment and water column, and the concentration of potentially

harmful elements (e.g. Cu, Zn and Al). We sought to answer the questions: (1) are there macrophyte species presently occurring only under specifically low or high values of important physical (current velocity) and chemical state factors (availability of N and P) or a low or high degree of anthropogenic influence on river morphology, and (2) which investigated variables differ significantly between the recognizable species assemblages at the reach level?

Materials and methods

Study area

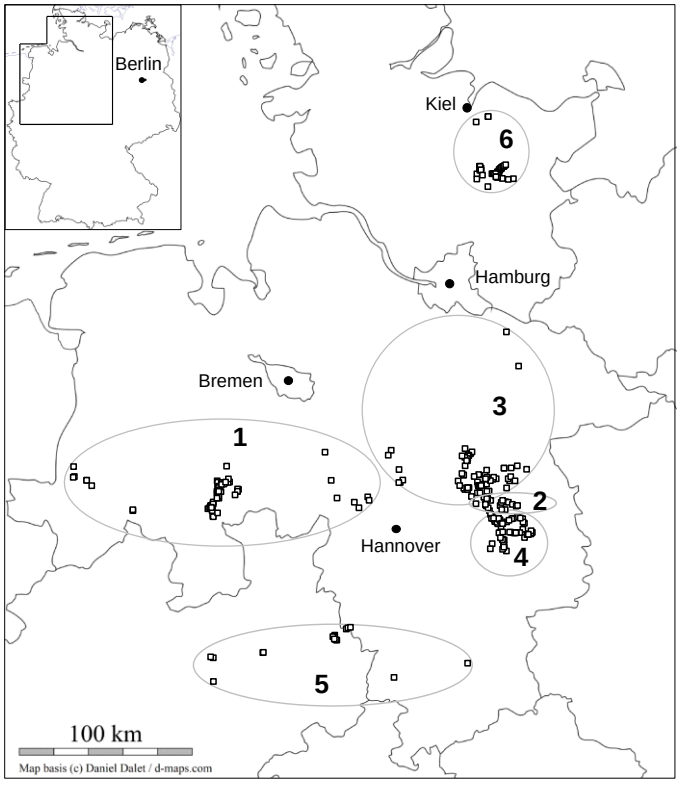

Figure 2.1 Location of the 291 study plots (open squares) in the six study regions of the north-west German lowlands. 1 = Ems-Hunte moraine country, 2 = Aller lowlands, 3 = Lüneburg Heath, 4 = northern Harz foothills, 5 = base of the Weser-Leine uplands and 6 = Eastern Holstein moraine country

The study area is situated in the Pleistocene lowlands of north-west Germany in the states of Lower Saxony, Schleswig-Holstein and North-Rhine-Westphalia at elevations below 210 m a.s.l. Six study regions with a large number of rivers and streams were selected: 1. the Ems-Hunte moraine country; 2. the Aller lowlands; 3. the Lüneburg Heath; 4. the northern Harz foothills; 5. the basis of the Weser-Leine uplands, and 6. the Eastern Holstein moraines (Figure 2.1). While the river sediments of the study regions 1, 2 and 3 are base-poor, those

of the regions 4, 5 and 6 are moderately base-rich (Table 2.1). The six regions belong to different catchment areas: In region 1, 81 % of the plots are located in the Hunte catchment, 13 % in the Ems catchment; all plots of region 2 refer to the Aller catchment; in region 3, 92 % of the plots are associated with the right-side Aller tributaries, 8 % refer to tributaries of river Elbe; in region 4, 97 % of the plots belong to the Oker catchment; in region 5, 77 % belong to the Leine-Weser system, 23 % to the Rhine catchment; the water courses in region 6 drain into the Baltic Sea and not into the North sea as in all other regions investigated. All rivers receive considerable nutrient loads from the adjacent intensively managed agricultural land. We established a total of 291 study plots in 69 rivers and streams, covering a broad range of water courses of different sizes (1–75 m width and 0.2–>2 m depth), current velocities (from close to zero to 50 cm s^{-1}) and sediment types (sandy or loamy with partial coverage by organic deposits, gravel or stones). The catchments of all rivers are part of the cultural landscape of north-west Germany, which consists of a mosaic of arable fields, pastures, meadows, forests and settlements. Due to the oceanic influence, the north-west German lowlands have a humid climate, characterized by warm summers and relatively mild winters with short frost periods. Mean annual temperatures range around 9 °C, with lowest mean temperatures in January (0.4 °C Braunschweig, Lower Saxony) and highest mean temperatures in July (17.2 °C for Hannover, Lower Saxony). The average annual precipitation lies between 656 mm yr^{-1} (Hannover) and 754 mm yr^{-1} (Kiel, Schleswig-Holstein; Deutscher Wetterdienst 2013).

Table 2.1 The six study regions with some characteristics (altitudinal range, minima and maxima of river width and water and sediment pH). The dominating substrate types and the most intensively studied rivers are indicated as well

Region	No. of studied rivers	Altitude [m a.s.l.]	River width [m]	Dominating substrate type	pH (water column)	pH (sediment)	Most intensively studied rivers (no. of plots)
Ems-Hunte	19	15–50	1–75	Sand	6.7–9.1	6.3–7.7	Hunte (28), Elze (5), Lohne (5)
Aller lowlands	1	30–60	8–40	Sand	8.1–9.1	6.2–7.6	Aller (14)
Lüneburg Heath	23	30–60	1–25	Sand	6.7–9.1	4.7–7.4	Lachte (12), Örtze (12)
Harz foothills	12	45–160	1–30	Sand	7.2–9.1	6.7–8.0	Schunter (28), Oker (27)
Weser-Leine uplands	9	90–210	3–30	Gravel	7.5–8.4	6.8–7.5	Emmer (6), Niese (3)
Eastern Holstein	5	25–40	2–45	Sand	7.2–8.5	6.6–7.7	Kossau (22), Schwentine (10)

Sampling design and field methods

The sampling design used locations where vegetation relevés had been taken in representative macrophyte stands in the 1930s–1960s (Roll 1939, Weber-Oldecop 1969, R. Tüxen archive: Hoppe 2005); these relevés were analyzed for vegetation change in an earlier study (Steffen et al. 2013). At each of the 291 locations, vegetation was sampled in 2010 or 2011 in plots of 100 m²; the relevés were quadratic if possible. This size was chosen as a compromise because smaller plots are not appropriate for adequately recording river macrophytes that can reach a length of several metres (e.g. *Ranunculus fluitans*), while larger plots would cover significant environmental gradients in smaller streams (e.g. sediment heterogeneities, Clarke and Wharton 2001). In addition, plot size in most cases exceeded the minimum sampling area required for macrophyte assemblages in streams of up to 10 m width according to the study of Wiegleb (1983) who found no increase in the number of hydrophyte species in reaches varying between 8 and 250 m length. Vegetation sampling took place between June and September 2010 and between June and August 2011. All species that rooted below the water level were noted. Cover values were mostly estimated in percent; in a few cases, the traditional Braun-Blanquet scale was used (Dierschke 1994). In every vegetation plot, one 100 ml sediment sample and one 50 ml water sample were taken close to the centre of the water course; the water samples were collected 10 cm below the water surface. Water and sediment sampling took place in all regions in June 2011 (except for region 6: August 2011). Water and sediment samples were cooled immediately and frozen on the same day for storage until analysis. At each plot, the width and depth of the water body were noted and current velocity in the main current was determined using a floating body and a stopwatch (drift method, Weber-Oldecop 1969). The anthropogenic influence on the riverbed morphology was estimated with a 5-category assessment scheme of naturalness after Brunken (1986) (1 = natural structurally diverse water course, 2 = richly structured water course, recognizably impacted by humans, 3 = straightened water course with numerous natural elements such as pools and rifles, 4 = straightened water course with a trapezoid cross profile, and 5 (combining categories 5 and 6 of Brunken's system) = completely modified water course structure with artificial bottom and/or bank substrates). Sediment type and type of adjacent vegetation were recorded. Herbarium specimens of all *Ranunculus* spp. as well as of critical taxa of *Potamogeton* were collected for later identification. Fresh plant material of *Callitriche* spp. was collected for identification by an experienced taxonomist.

Water analyses

The pH was measured with a pH meter (EASY pH, WTW, Weilheim, DE). The concentrations of aluminum, calcium, copper, iron, magnesium, manganese, potassium,

sodium, sulphur and zinc were analysed using ICP-OES (Optima 5300 DV, Perkin Elmer, Rodgau, DE). The concentrations of nitrate, ammonium and phosphate were determined with a Continuous Flow Analyzer (San^{Plus}, photometer SA 6250, Skalar Analytical B.V., Breda, NL).

Sediment analyses

The pH was measured in the moist suspension of the original sediment samples with a pH meter (EASY pH, WTW, Weilheim, DE). For further analyses, the sediment samples were filtered until dropping stopped and passed through a 2 mm sieve. One part of a sample was dried in a cabinet dryer at 70 °C for 48 h. The concentrations of total carbon (C_{total}) and total nitrogen (N) in the sediment material and of inorganic carbon (C_{inorg}) in the ash were determined with a C/N-autoanalyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, DE). For obtaining the C_{org}/N_{tot} ratio, C_{org} was calculated by subtracting C_{inorg} from C_{total} with C_{inorg} being measured in the ash after ignition of the sediment material at 950 °C. For determining the salt-extractable concentration of cations in the sediment, 2.5 g of a sediment sample were percolated with 100 ml of 0.2 N $BaCl_2$-solution and the concentrations of Al^{3+}, Ca^{2+}, Cu^{2+}, Fe^{2+}, Mg^{2+}, Mn^{2+}, K^{+}, Na^{+} and Zn^{2+} in the percolate being measured by ICP-OES. We used the resin-bag method for obtaining an estimate of plant-available phosphorus in the sediment; 1 g of a sediment sample was shaken with a resin bag (4 cm³ anion exchange resin (Dowex 1x8-50, The Dow Chemical Company, Midland, US) sewn in a polyethylene sieve cloth) for 16 h, the adsorbed P was subsequently re-exchanged by 10 % NaCl and 2 % NaOH solutions and the P concentration in the washing solution determined photometrically at 712 nm (Libra S22 UV/Vis spectrophotometer, Biochrom Ltd., Cambridge, GB).

Statistical analyses

In the statistical analyses at the species level, all 291 relevés were included and a total of 31 macrophyte species with a minimum occurrence in 10 plots considered. A Wilcoxon test was used to test for differences between all sites with the occurrence of a species against the sites where the species was absent. Simple logistic regressions were performed with species presence/absence data and environmental variables and tested with an omnibus-test to obtain predicted probabilities of species occurrence at a certain parameter value. Analyses at the community level were performed with 47 macrophyte species that occurred at least in five plots. In these analyses, only relevés that contained a minimum of two taxa were included (280). Vegetation classification was done with cluster analysis (Sørensen distance measure, linkage: beta -0.25). Differences in mean values between the eight cluster groups were tested for significance with a Tukey post hoc test. To identify the most relevant

variables, simple and multiple correlation analyses with backward variable selection were conducted. A Principal Components Analysis (PCA) on the environmental data was also performed to investigate inter-correlations, but the results are not presented, because the explanatory value of the first three components was rather weak (35 %). In the following variables, each two or three of them were strongly correlated to each other (correlation coefficient >0.70); river width and depth; Na and K concentration (water); Na and K concentration (sediment); Ca, Mg and S concentration (water); Ca and Mg concentration (sediment); N, C and C_{org} concentration (sediment). Thus, only one of these variables each was kept in the analyses.

Diversity was expressed by means of true diversity D (Jost, 2006), $D= e^{H'}$, with H' being Shannon's diversity index and D the number of species that would be needed to produce the given Shannon diversity value, if cover values were evenly distributed. Red-listed species were identified using the red list for ferns and flowering plants of Germany (Korneck et al. 1996). Plant growth forms were determined after Segal (1968), Mäkirinta (1978) and Wiegleb (1991). An indicator species analysis (ISA) after Dufrêne and Legendre (1997), where indicator values are generated from a combination of a species' abundance and frequency in a particular group, was carried out with PCOrd 5.1 (MjM Software Design, Gleneden Beach, US). The ISA was performed with eight groups and indicator values were assessed for significance using Monte Carlo randomizations with 10000 permutations. A detrended correspondence analysis (DCA, Hill and Gauch 1980), where environmental variables were added in a post hoc manner, was done with Canoco 4.56 (Plant Research International, Wageningen, NL). For statistical tests and correlation analyses, the package SPSS 15.0 (SPSS Inc., Chicago, US) was used.

Results

Species level

In total, 94 macrophyte species were recorded, including hydrophytes, amphiphytes and helophytes that rooted in the river bed. The most abundant species were *Lemna minor* (occurrence in 192 of 291 plots), *Sparganium emersum* (169 plots), *Phalaris arundinacea* (161 plots), *Callitriche platycarpa* (108 plots), *Spirodela polyrhiza* (107 plots) and *Nuphar lutea* (93 plots).

Twelve species were found to predominantly occur in habitats of generally large, deep river reaches with low current velocities (Table 2.2 in Appendix). Of those, habitats of *Elodea nuttallii*, *Myriophyllum spicatum*, *Nuphar lutea*, *Sagittaria sagittifolia* and *Spirodela polyrhiza* were base- and nutrient-rich (Table 2.3, Figures 2.2a and 2.2b). *Hydrocharis morsus-ranae* and *Potamogeton crispus* occurred in more or less alkaline environments, while *Ceratophyllum demersum*, *Lemna minor* and *Sparganium emersum* preferred nutrient-rich

habitats. The occurrence of *E. nuttallii* and *L. gibba* was related to high turbidity. Of the group of species that were mostly found in potamal reaches, *Potamogeton lucens* and six other species were associated with low Al concentrations in water and/or sediment.

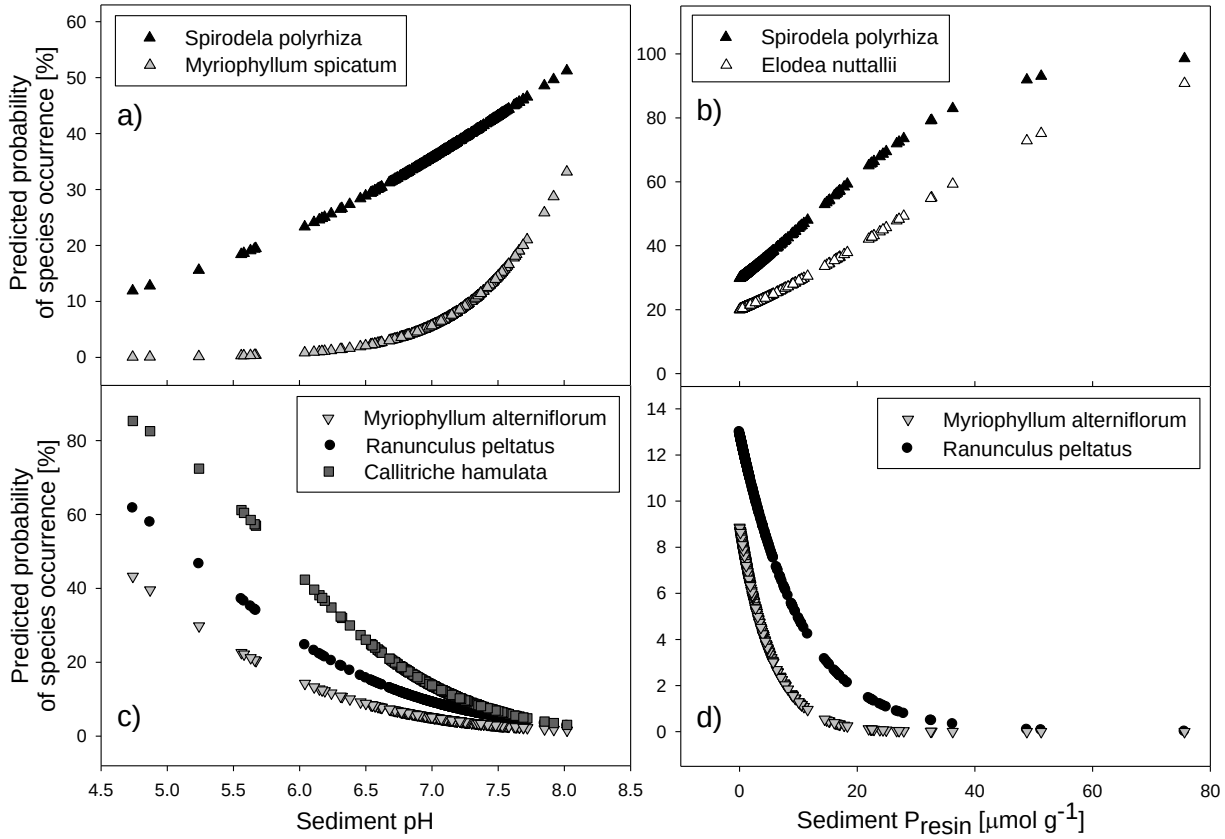

Figure 2.2 Predicted probabilities of occurrence of *Callitriche hamulata*, *Elodea nuttallii*, *Myriophyllum alterniflorum*, *M. spicatum*, *Ranunculus peltatus* and *Spirodela polyrhiza* at different pH values and concentrations of plant-available phosphorus (P_{resin}) in the sediment (significance levels of the logistic regressions: Table 2.3)

Seven species were found in reaches that were small and shallow, had a close-to-natural structure and were characterized by fast flowing water. Of those, *Callitriche hamulata*, *Myriophyllum alterniflorum* and *Ranunculus peltatus* were related to a significantly lower sediment pH, lower water and sediment Ca concentration, lower sediment K and Na as well as lower water and sediment Mg concentrations than at the sites where the species were absent (Figure 2.2c). The latter two species were also related to a low P concentration in the sediment (Figure 2.2d). *Berula erecta* and *Glyceria fluitans* occurred in habitats characterized by low sediment pH values and low Ca, P and Fe concentrations of the sediment. *Fontinalis antipyretica* occurred in habitats of low sediment N and P contents, showing a significantly higher water Mg concentration, compared to sites without the species. *Sparganium erectum*

occurred mostly in base-rich habitats. Four species of this group showed an apparent affinity to a high sediment Al concentration.

Behaving indifferently towards water course morphology, *Elodea canadensis*, *Callitriche obtusangula* and *C. platycarpa* were associated with soft water, while *Butomus umbellatus*, *Lemna trisulca*, *Potamogeton natans*, *P. pectinatus* and *Utricularia vulgaris* occurred in Ca-rich waters. The species *Phalaris arundinacea*, *Phragmites australis*, *Potamogeton perfoliatus* and *P. pusillus* behaved indifferently towards the various parameters studied.

Table 2.3 Results of the omnibus-test for logistic regressions (chi² and p) on six selected hydrophyte species and selected environmental variables. Significant correlations (at p<0.1) and their directions are indicated: ↓ for negative and ↑ for positive relation. CEC – cation exchange capacity

	Current velocity	**pH (Sed.)**	**C_{tot} (Sed.)**	**C_{org} (Sed.)**	**NH_4^+ (Wat.)**	**NO_3^- (Wat.)**	**N_{tot} (Sed.)**	**P_{resin} (Sed.)**	**K (Sed.)**	**Na (Wat.)**	**Na (Sed.)**	**CEC**
Callitriche hamulata												
Chi^2		↓ 21.3	↓ 4.0		↓ 6.1		↓ 3.9			↓ 4.1	↓ 4.0	↓ 8.0
p		<0.001	0.046		0.014		0.049			0.043	0.045	0.005
Myriophyllum alterniflorum												
Chi^2	↑ 5.1	↓ 6.6	↓ 14.8	↓ 11.9	↓ 8.0		↓ 7.3	↓ 5.5	↓ 5.7	↓ 6.2	↓ 7.0	↓ 16.4
p	0.024	0.010	<0.001	0.001	0.005		0.007	0.019	0.017	0.013	0.008	<0.001
Ranunculus peltatus												
Chi^2		↓ 10.6	↓ 7.2	↓ 3.9		↑ 4.8	↓ 3.9	↓ 5.1	↓ 18.6	↓ 20.7	↓ 7.3	↓ 19.1
p		0.001	0.007	0.049		0.029	0.050	0.023	<0.001	<0.001	0.007	<0.001
Elodea nuttallii												
Chi^2	↓ 9.0		↑ 7.0	↑ 11.3			↑ 10.7	↑ 10.1	↑ 3.4			
p	0.003		0.008	0.001			0.001	0.001	0.064			
Myriophyllum spicatum												
Chi^2	↓ 3.8	↑ 9.0				↑ 2.9			↑ 11.6	↑ 16.3	↑ 11.2	
p	0.051	0.003				0.088			0.001	<0.001	0.001	
Spirodela polyrhiza												
Chi^2	↓ 19.0	↑ 4.2	↑ 14.1	↑ 22.9	↑ 30.8	↓ 28.3	↑ 24.7	↑ 16.5	↑ 3.2	↓ 7.0		↑ 28.1
p	<0.001	0.040	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.075	0.008		<0.001

Community level

Species richness per relevé ranged between two and 15. Plot-level species diversity (D) did not show a significant correlation with any of the measured environmental variables (all correlation coefficients <0.25). The river macrophyte vegetation was grouped into eight clusters by the cluster analysis. Each cluster is characterized by indicator species according to the indicator species analysis (Table 2.4). Cluster **C** is characterized by *Nuphar lutea, Potamogeton natans* and *Spirodela polyrhiza*, cluster **D** by *Elodea nuttallii* and *Lemna gibba*. The pleustophytic (lemnid, ricciellid and ceratophyllid) and nymphaeid growth forms were grouped in these two clusters, which are mainly found in the Ems-Hunte region (Figure 2.3). Clusters **C** and **D** corresponded to potamal reaches (Figures 2.4a and 2.4b) with high C_{org}, N and P concentrations in the sediment (Figures 2.4c and 2.4d), low water Al concentration, but high pH and a modified morphological structure of the river bed. These two clusters are characterized by high species richness, high plant coverage and, in the case of cluster **C,** by a relatively high proportion of red-listed species per relevé (16 %) as well as high diversity (D). Cluster **B** is characterized by *Sparganium erectum*, *Potamogeton crispus* and *Potamogeton pectinatus*. The parvopotamids are grouped in this cluster. Assemblages of this cluster mainly occurred in the northern Harz foothills and in Eastern Holstein. It includes a moderately species-rich and diverse community found in habitats with low current velocity, high Na and Zn concentrations as well as a rather high pH of the water (Figures 2.4e and 2.4f). Cluster **E** is characterized, among others, by *Myriophyllum alterniflorum* and *Ranunculus peltatus*. This assemblage contains the batrachid species and is moderately species-rich. It prevails in the Lüneburg Heath and the northern Harz foothills regions. It grows in small, shallow reaches with fast flowing water, low sediment C_{org}, N and P contents as well as low water Na, Zn and pH. Together with cluster **F**, which is characterized by *Fontinalis antipyretica* and *Nasturtium officinale*, and cluster **A**, characterized by *Sparganium emersum*, *Callitriche hamulata* and *Myriophyllum spicatum*, these three clusters contain all myriophyllid and peplid species. Cluster **A**‘s community was mainly found in the Lüneburg Heath region in reaches that had a relatively unmodified structure and rather low current velocities. The sediments were of low Ca, C_{total} and C_{org} as well as low N concentrations. Cluster **H** with dominant *Phragmites australis* was mainly present in the Eastern Holstein region. It comprises the most species-poor community in habitats of low sediment P and high Ca concentrations, but low water nitrate content and low pH (Figures 2.4g and 2.4h). The reaches of this community had a close-to-natural structure. The habitats of the vegetation grouped in the clusters **F** and **G**, which occurred mainly in the Lüneburg Heath and northern Harz foothills regions, were characterized by rather high current velocities. They did not show any extremes in other environmental parameters.

Table 2.4 The macrophyte vegetation of the study region as classified into eight assemblages by cluster analysis (in order of increasing adaptation to life in water from A: submerged growth forms, to H: helophytes). Base figures: relative frequency of species occurrence within a cluster in percent; exponents: cover values as averages within clusters. Indicator species for each cluster were derived from the indicator species analysis

No. of relevés		29	26	78	14	26	46	52	9
No. of species		33	36	42	31	31	42	40	12
No. of species/relevé		6.6	7.5	8.9	8.4	6.8	5.8	6.3	3.6
Indicator species [2)]	**Growth form [1)]**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Cluster A									
Spar. emer.*	Val.	100 $^{24.5}$	54 $^{6.3}$	50 $^{3.6}$	64 $^{2.7}$	38 $^{1.8}$	33 $^{1.7}$	94 $^{2.3}$	33 $^{0.8}$
Call. hamu.*	Pep.	45 $^{2.8}$	-	6 $^{1.3}$	14 $^{0.1}$	19 $^{1.3}$	15 $^{1.4}$	19 $^{1.1}$	-
Myri. spic.*	Myr.	21 $^{10.3}$	19 $^{1.6}$	6 $^{1.8}$	-	-	4 $^{3.0}$	10 $^{2.9}$	-
Call. stag.	Pep.	14 $^{0.5}$	8 $^{0.4}$	1 $^{1.0}$	-	-	-	4 $^{0.6}$	-
Pota. perf.	M-pot.	10 $^{5.0}$	4 $^{7.0}$	1 $^{4.0}$	14 $^{0.3}$	4 $^{2.5}$	2 $^{35.0}$	4 $^{1.5}$	11 $^{2.0}$
Cluster B									
Spar. erec.*	Hel.	21 $^{1.9}$	58 $^{20.2}$	42 $^{2.9}$	21 $^{0.3}$	19 $^{1.6}$	17 $^{1.3}$	38 $^{2.9}$	-
Pota. pect.*	P-pot.	24 $^{2.8}$	54 $^{21.5}$	10 $^{2.5}$	7 $^{25.0}$	-	2 $^{0.0}$	10 $^{3.8}$	-
Pota. cris.*	P-pot.	7 $^{0.5}$	38 $^{5.2}$	6 $^{0.7}$	14 $^{7.0}$	8 $^{0.3}$	7 $^{1.5}$	6 $^{0.6}$	-
Buto. umbe.*	Val./Hel.	10 $^{2.7}$	23 $^{8.1}$	23 $^{1.9}$	7 $^{0.0}$	-	-	12 $^{1.5}$	11 $^{1.0}$
Phal. arun.	Hel.	52 $^{1.3}$	81 $^{2.0}$	54 $^{2.0}$	79 $^{1.4}$	58 $^{1.9}$	74 $^{1.7}$	42 $^{0.8}$	11 $^{3.0}$
Cluster C									
Nuph. lute.*	Nym.	7 $^{0.4}$	23 $^{1.8}$	73 $^{13.8}$	29 $^{8.1}$	4 $^{10.0}$	7 $^{2.3}$	37 $^{2.3}$	11 $^{0.5}$
Sagi. sagi.*	Val./Hel.	17 $^{14.5}$	23 $^{4.3}$	72 $^{13.9}$	29 $^{5.5}$	-	7 $^{0.4}$	17 $^{1.5}$	-
Spir. poly.*	Lem.	21 $^{0.0}$	38 $^{0.3}$	64 $^{3.9}$	79 $^{0.6}$	4 $^{0.5}$	26 $^{0.6}$	21 $^{0.0}$	67 $^{0.0}$
Utri. vulg.*	Cer.	-	-	13 $^{4.3}$	-	-	-	-	-
Pota. nata.*	Nym.	17 $^{14.2}$	4 $^{4.0}$	31 $^{13.3}$	14 $^{0.6}$	-	2 $^{1.0}$	6 $^{1.9}$	-
Pota. pusi.*	P-pot.	-	-	13 $^{5.3}$	-	-	-	-	-
Pota. luce.*	M-pot.	3 $^{1.5}$	-	14 $^{20.0}$	-	-	-	2 $^{2.0}$	-
Glyc. maxi.*	Val./Hel.	7 $^{0.5}$	12 $^{1.5}$	33 $^{5.1}$	36 $^{1.4}$	23 $^{2.4}$	22 $^{1.1}$	13 $^{0.7}$	-
Lemn. mino.	Lem.	72 $^{0.1}$	77 $^{0.5}$	91 $^{1.8}$	86 $^{0.5}$	35 $^{1.8}$	41 $^{2.3}$	63 $^{0.1}$	78 $^{0.0}$
Hydr. mors.	Hyd.	-	8 $^{0.3}$	9 $^{2.2}$	7 $^{0.1}$	4 $^{0.5}$	2 $^{2.0}$	-	-
Lemn. tris.	Ric.	3 $^{0.1}$	15 $^{0.2}$	18 $^{0.2}$	21 $^{0.0}$	8 $^{0.5}$	9 $^{0.0}$	6 $^{0.0}$	11 $^{0.0}$
Cera. deme.	Cer.	-	12 $^{2.8}$	19 $^{2.5}$	21 $^{1.2}$	-	4 $^{25.1}$	-	-
Cluster D									
Elod. nutt.*	Elo.	10 $^{3.3}$	12 $^{0.5}$	49 $^{2.1}$	100 $^{35.7}$	4 $^{0.5}$	11 $^{2.0}$	13 $^{1.5}$	-
Lemn. gibb.*	Lem.	3 $^{0.0}$	19 $^{0.1}$	21 $^{1.3}$	29 $^{2.3}$	8 $^{1.0}$	2 $^{3.0}$	2 $^{0.0}$	11 $^{0.1}$
Pers. amph.	Nym.	-	4 $^{0.5}$	13 $^{0.6}$	14 $^{1.0}$	-	2 $^{0.1}$	2 $^{0.5}$	-
Iris pseu.	Hel.	-	-	1 $^{0.2}$	7 $^{0.2}$	-	2 $^{0.4}$	6 $^{0.3}$	-
Cluster E									
Beru. erec.*	Hel.	28 $^{1.5}$	12 $^{1.0}$	10 $^{1.8}$	-	62 $^{16.1}$	20 $^{2.2}$	25 $^{1.5}$	-
Call. plat.*	Pep.	41 $^{1.0}$	27 $^{0.7}$	41 $^{1.1}$	21 $^{0.3}$	62 $^{7.5}$	35 $^{2.0}$	42 $^{0.9}$	-
Plat. ripa. (M)*	Bry.	-	12 $^{1.2}$	-	-	38 $^{20.4}$	9 $^{0.3}$	4 $^{0.3}$	-
Ranu. pelt.*	Bat.	10 $^{3.1}$	-	3 $^{0.6}$	14 $^{10.0}$	38 $^{12.4}$	4 $^{1.5}$	17 $^{1.7}$	-
Ment. aqua.*	Hel.	7 $^{1.8}$	8 $^{2.6}$	1 $^{0.3}$	-	42 $^{5.2}$	11 $^{0.7}$	10 $^{0.8}$	11 $^{1.0}$
Vero. becc.*	Hel.	-	4 $^{0.2}$	4 $^{0.6}$	7 $^{1.0}$	27 $^{0.9}$	20 $^{0.5}$	6 $^{0.2}$	-
Myos. palu.*	Hel.	14 $^{0.3}$	27 $^{0.3}$	27 $^{0.9}$	7 $^{1.0}$	54 $^{0.6}$	26 $^{0.7}$	12 $^{0.3}$	11 $^{0.1}$
Myri. alte.	Myr.	10 $^{0.6}$	-	3 $^{1.5}$	-	19 $^{1.5}$	2 $^{0.3}$	10 $^{3.0}$	-
Agro. stol.	Val./Hel.	24 $^{0.8}$	19 $^{0.2}$	4 $^{0.3}$	7 $^{0.5}$	23 $^{1.1}$	22 $^{0.6}$	10 $^{0.2}$	-
Alis. plan.	Hel.	-	-	10 $^{0.3}$	7 $^{0.4}$	4 $^{5.0}$	2 $^{0.1}$	-	-
Cluster F									
Font. anti. (M)*	Bry.	3 $^{1.0}$	4 $^{0.3}$	-	-	15 $^{0.7}$	24 $^{5.2}$	4 $^{0.6}$	-
Nast. offi.*	Hel.	10 $^{0.2}$	4 $^{0.0}$	5 $^{4.1}$	-	19 $^{1.0}$	20 $^{12.5}$	2 $^{0.2}$	-
Ranu. flui.	Myr.	-	-	-	-	-	9 $^{13.4}$	2 $^{1.5}$	-

No. of relevés		29	26	78	14	26	46	52	9
No. of species		33	36	42	31	31	42	40	12
No. of species/relevé		6.6	7.5	8.9	8.4	6.8	5.8	6.3	3.6
Indicator species [2)]	**Growth form [1)]**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Chil. poly. (M)	Bry.	-	-	-	-	4 $^{2.0}$	7 $^{6.8}$	2 $^{0.1}$	-
Elod. cana.	Elo.	24 $^{3.8}$	15 $^{4.0}$	27 $^{1.6}$	50 $^{1.1}$	23 $^{1.7}$	26 $^{14.5}$	27 $^{0.5}$	-
Ranu. tric.	Myr.	-	4 $^{11.0}$	-	-	-	11 $^{2.2}$	2 $^{0.3}$	-
Glyc. flui.	Val./Hel.	10 $^{9.5}$	8 $^{0.6}$	4 $^{2.5}$	7 $^{0.1}$	12 $^{0.5}$	15 $^{5.8}$	8 $^{1.7}$	-
Vero. anag.	Hel.	3 $^{0.4}$	4 $^{0.3}$	3 $^{0.3}$	7 $^{0.0}$	4 $^{0.5}$	13 $^{0.2}$	-	-
Call. obtu.	Pep.	-	-	8 $^{1.0}$	21 $^{0.5}$	4 $^{4.0}$	4 $^{18.5}$	-	-
Cluster G									
Acor. cala.	Hel.	-	8 $^{0.5}$	3 $^{0.9}$	-	-	7 $^{0.4}$	13 $^{0.6}$	-
Cluster H									
Phra. aust.*	Hel.	7 $^{1.0}$	15 $^{2.3}$	1 $^{0.6}$	-	-	9 $^{3.3}$	10 $^{1.6}$	100 $^{10.8}$

[1)] Bat. = batrachid, Bry. = bryid, Cer. = ceratophyllid, Elo. = elodeid, Hel. = helophytic, Hyd. = hydrocharid, Lem. = lemnid, M-Pot = magnopotamid, Myr. = myriophyllid, Nym = nymphaeid, Pep. = peplid, P-pot. = parvopotamid, Ric. = ricciellid, Val. = vallisnerid

[2)] * = significant indicator species for the respective cluster ($p<0.05$), (M) = moss

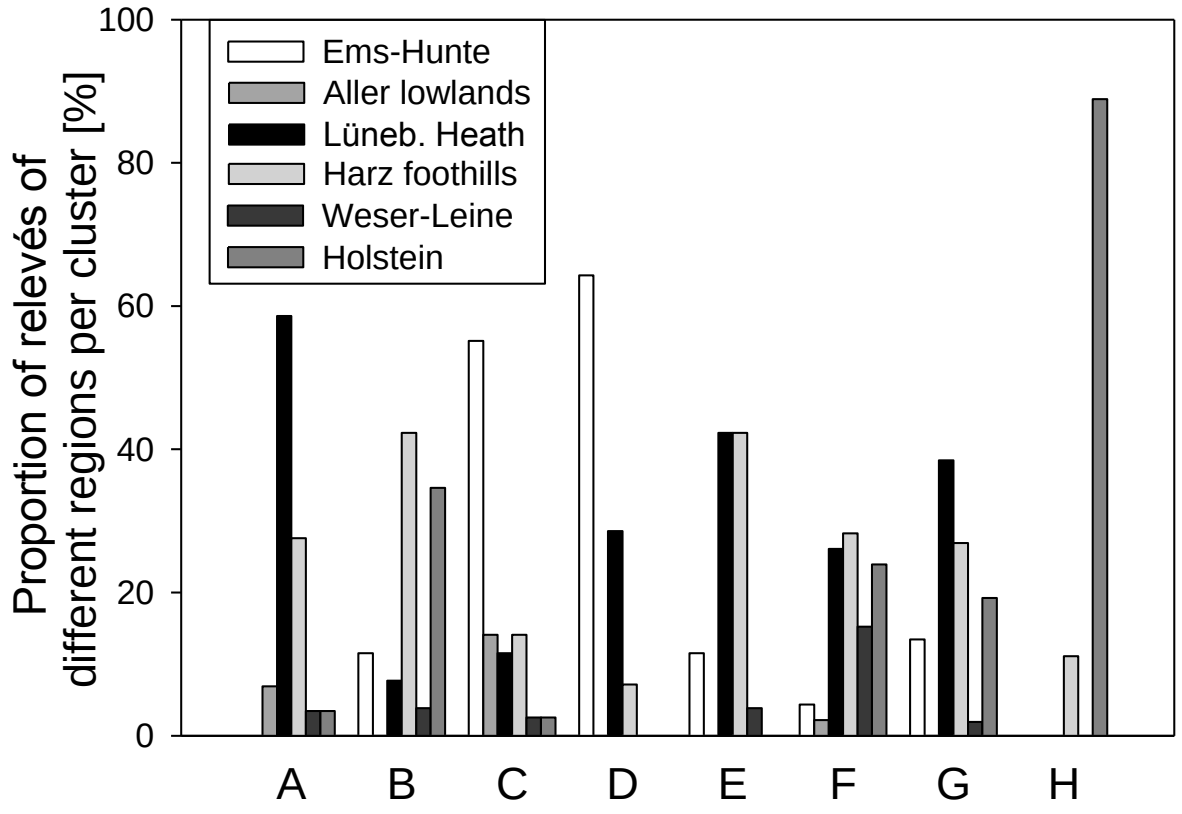

Figure 2.3 Relative contribution (in %) of relevés from the six study regions to the total number of relevés in the eight vegetation clusters A to H

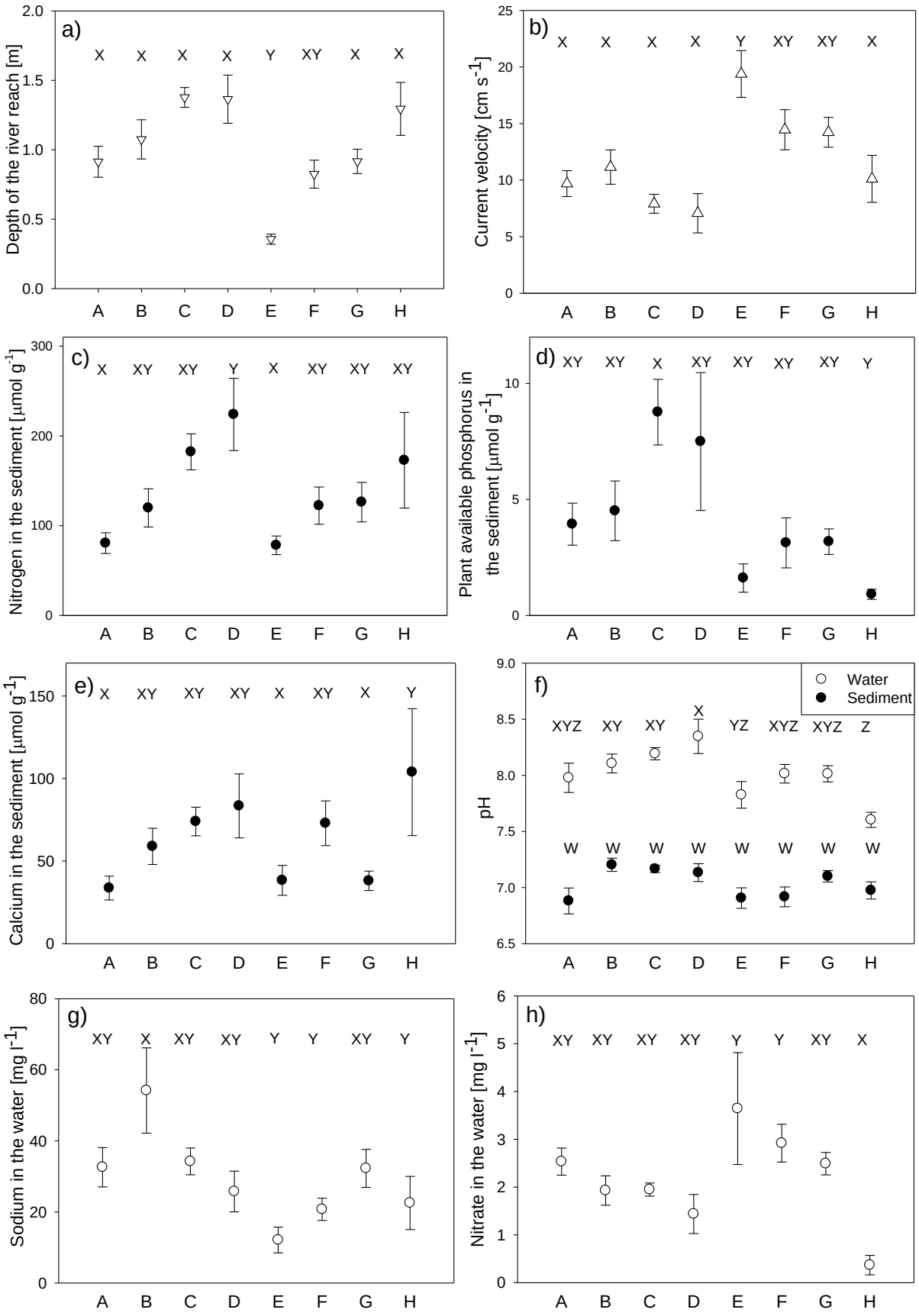

Figure 2.4 a) Depth of water body, b) current velocity, sediment contents of c) total N, d) plant available P (P_{resin}) and e) calcium, f) pH (water and sediment) and g) sodium and h) nitrate in the water in eight macrophyte vegetation clusters (A to H). Means ± SE of nine to 78 plots sampled in June or August 2011. Different letters (W to Z) indicate significant differences between the vegetation clusters

Of the variables that were identified as being relevant for macrophyte community composition according to multiple regression analysis with backward variable selection, current velocity showed a strong positive correlation with DCA axis 1, water depth a negative one (Figure 2.5, Table 2.5 in Appendix). The P, C_{org} and Ca concentrations in the sediment, the NH_4, Fe and Na concentrations in the water and the anthropogenic influence on the river bed structure were negatively correlated with this axis. The second DCA axis was positively correlated with the pH of the sediment and negatively with the Zn concentration in the water.

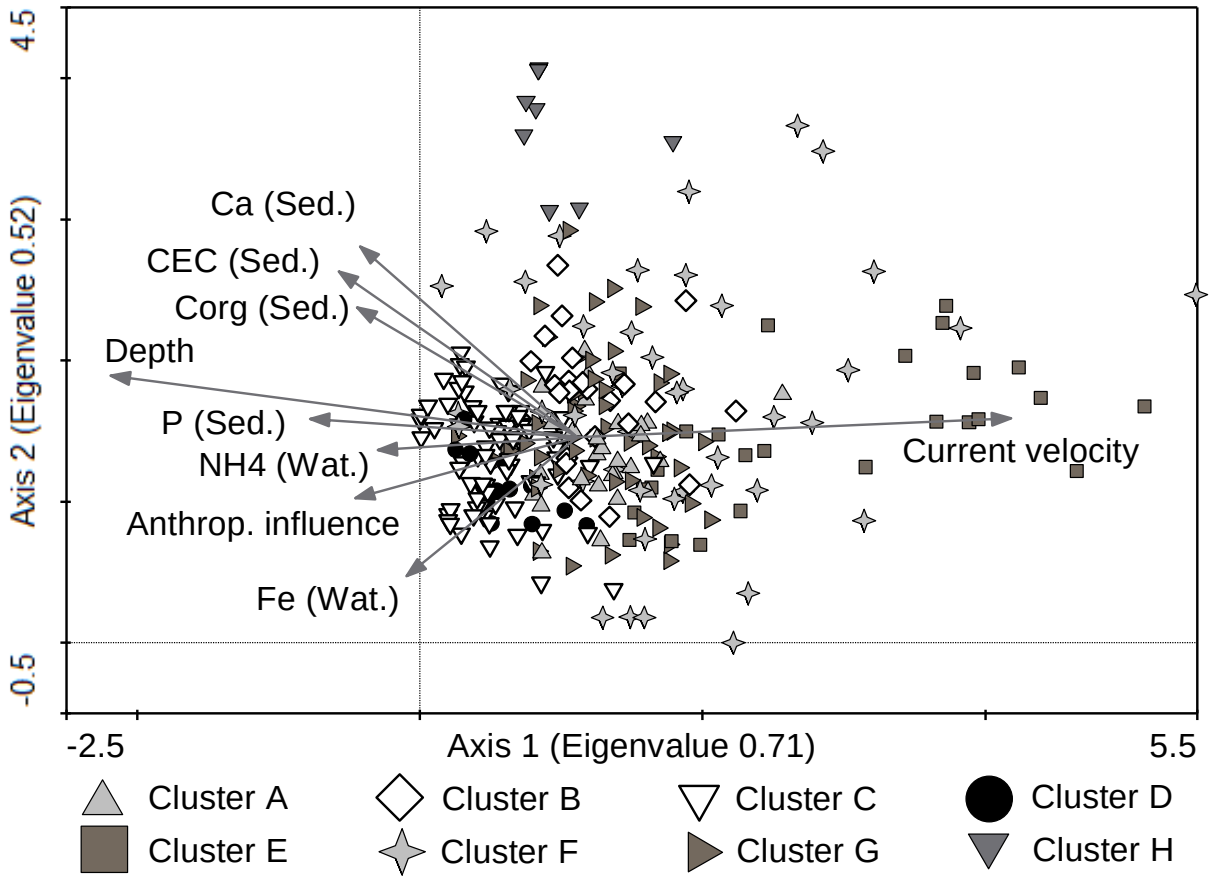

Figure 2.5 DCA of the clustered vegetation (280 relevés, eight groups) and selected environmental variables (Wat. = measured in the water column, Sed. = measured in the sediment). For the ordination, species cover values were log-transformed

Discussion

We focused on a comprehensive analysis of the effects of physical and chemical parameters on community assembly and species distribution of river macrophytes. In order to avoid false conclusions based on pseudocorrelation, we analyzed more than 30 variables including their intercorrelations. At the community level in the six regions, we found seven groups of true macrophyte assemblages in which free-floating species and hydrophytes with submerged or floating leaves rooting in the sediment were dominant. One additional cluster refers to a helophytic community characterized by *Phragmites australis*. The seven species

assemblages show a marked differentiation according to the main river habitats colonized by them and also with respect to the relative abundance of macrophyte growth forms. Three clusters are related to nutrient-rich, potamal water course reaches. One of them (cluster B) contains the parvopotamid species including *Potamogeton crispus* and *P. pectinatus* that are known as eutraphent species (Casper and Krausch 1980). Another two clusters (C and D) contain the pleustophytic and nymphaeid species of the regional species pool. Relevés assigned to those species-rich clusters were mainly taken in the Ems-Hunte region, where the river macrophyte assemblages had earlier been characterized by their abundance of nymphaeid species (Herr et al. 1989, Zander et al. 1992). In eutrophic waters that are often turbid due to phytoplankton blooms, the pleustophytic and nymphaeid growth forms are advantageous, because these plants place their leaves close to or on the water surface and thus escape light competition in the water column (Mesters 1995). In correspondence with the species level analysis, the indicator species for highly eutrophic conditions *Elodea nuttallii* and *Spirodela polyrhiza* are characteristic species of these two clusters. One cluster (E) contains the species *Myriophyllum alterniflorum* and *Ranunculus peltatus*, which were identified as regional indicators for mesotrophic conditions in our study region. Corresponding conclusions by Weber-Oldecop (1969) and Herr et al. (1989) can be generalized for a wider geographical area. Together with two other clusters (A and F), these three assemblages of less nutrient-rich running water reaches contain members of the batrachid, myriophyllid and peplid growth forms, which are adapted to relatively high current velocities. These assemblages are found in the study region mostly in the Lüneburg Heath confirming earlier work by Herr et al. (1989). A similar community with elodeid, peplid and batrachid species was also reported as typical for streams with mesotrophic, neutral conditions in northeast France (Thiébaut and Muller 1999). Cluster G is the second largest one containing more than 50 relevés that lack well-characterized indicative species. It may be termed a ‘central cluster’ in analogy to the ‘central association’ in phytosociology, because it contains ‘average’ relevés in which a dominance of a certain growth form is absent, specific dominance structures do not exist, and the relevés are neither particularly species-rich nor species-poor. This type of vegetation was called ‘*Sparganium emersum* community (various formations)’ by Herr et al. (1989, Tab. 16). In Danish lowland streams, the *Sparganium* community was the predominant vegetation cluster (Riis et al. 2000); the authors assume that the community is promoted by regular mowing. The eighth cluster (H) is only indicated by the helophyte *Phragmites australis* and is thus somewhat atypical for our macrophyte data set; this cluster includes less than ten species-poor relevés mainly from the Eastern Holstein region. However, *Phragmites*-dominated vegetation can frequently be found in river reaches off the main current, in particular around the Baltic Sea (Baattrup-Pedersen et al. 2003, Paal

et al. 2007). Emergent helophytes such as *Phragmites* are often excluded from sampling or analysis (see e.g. Demars and Harper 1998), as a low indicative value is expected.

The seven vegetation clusters were not only characterized by each one to eight indicator species and characteristic combinations of growth forms, but also by marked differences in certain physical, chemical and river morphological properties. According to the DCA, water depth and current velocity were the two factors with largest influence on the species composition of the studied streams and rivers. This result supports earlier findings that current velocity and related factors play a key role for the structure and composition of the macrophyte vegetation of running waters (see review by Franklin et al. 2008). Even though the informative value of instantaneous flow velocity measurements may be limited because seasonal variability is not captured, a rough classification of flow regimes may be possible, as the measurements were done in summer, when flow rates are typically lower than in winter and spring. The influence of water depth is plausible, because it determines the relative importance of helophytic and pleustophytic species. Chemical properties of the sediment were of secondary importance with P_{resin} apparently being the most influential element while N_{total} and the salt-exchangeable concentrations of Ca and Fe in the sediment played subordinate roles. Even less influential were the concentrations of nutrients and other elements in the water column. This agrees with the findings of Demars and Edwards (2009); it is not surprising for several reasons. First, concentrations typically vary considerably over time both diurnally and seasonally. Our data from summer 2011 give only a snapshot of the fluctuation in water chemistry, because the focus of our study was on the sampling of a large number of rivers and vegetation stands. In summer, phosphate and other nutrients are rapidly cycled through the aquatic community with the consequence that actual nutrient concentrations are rarely related to supply rates. Second, intercorrelation with other factors is high and possible effects are difficult to separate from each other (Demars and Harper 1998). In naturally nutrient-rich rivers (in particular of the regions 1, 4 and 6), a response to further nutrient enrichment is not very likely (Demars and Edwards 2009).

When comparing the means of our water chemistry data from 291 sampling locations with literature data from other North and Central European streams and rivers, we found in general good agreement (Remy 1993, Schneider and Melzer 2004, Paal et al. 2007). As the samples were mainly taken in June, when nutrient uptake by macrophytes and microalgae (phytoplankton and benthic forms) should be highest, the measured phosphate (mean: 0.03 mg L^{-1}), nitrate (2.35 mg L^{-1}) and ammonium (0.17 mg L^{-1}) concentrations in the water column were relatively low. In contrast, the sediment concentrations of macronutrients (N, P, Ca, K, Mg) were high at several sites, especially in the regions 1 (Ems-Hunte) and 6 (Eastern Holstein), where intensive agricultural land-use is ubiquitous and the sediment pools are reflecting the ‘long-term memory’ of the water body.

At the species level, a number of taxa differed significantly with respect to the physical and chemical properties of their habitats, which became visible when comparing sites with and without occurrence of the target species. The investigated running waters are all in a mesotrophic to eutrophic or even hypertrophic condition (LAWA 1998, NLÖ 2001). Within this range of water conditions, *Myriophyllum alterniflorum* and *Ranunculus peltatus* were present in relatively nutrient-poor habitats, as it was stated earlier by Wiegleb (1984) for northern German waters. At the same time, the habitats of these taxa can be categorized as 'rhithral', a term that is most often applied to headwaters flowing through mountainous regions, but also relates to lowland streams of high current velocities and low temperatures due to groundwater inflow (Weber-Oldecop 1970). In the lowlands, rhithral waters are generally not as nutrient-rich as potamal waters, because a river is enriched with nutrients between its close-to-spring rhithral range, where dilution has an effect on element concentrations when groundwater flows in, and its lower potamal range after the passage through an agricultural catchment area. Accordingly, the species *Elodea nuttallii*, *Myriophyllum spicatum* and *Spirodela polyrhiza*, which are generally used as indicators for eutrophic habitats, showed an affinity to potamal river reaches.

That flow velocity is a main structuring force of macrophyte assemblages in rivers, can be expected from the known large species differences in the tolerance of water movement (Sirjola 1969, Brewer and Parker 1990). Less clear are species differences in the response to chemical factors. Macrophyte species have been found to prefer different N forms which might explain some of the apparent affinities found. For example, a macrophyte species known to prefer ammonium is *Potamogeton alpinus* that has been observed to show reduced growth in nitrate-enriched water (Boedeltje et al. 2005). Another species with possible preference for NH_4^+ is *Elodea canadensis* (Melzer and Kaiser 1986, Rolland et al. 1999). Sewage dumping could promote species with ammonium preference. We found several species that were typically present at elevated NH_4^+ water concentrations, but showed no association to higher NO_3^- concentrations (e.g. *Ceratophyllum demersum, Sagittaria sagittifolia, Spirodela polyrhiza*). On the other hand, species such as *Potamogeton pectinatus, Myriophyllum spicatum, Callitriche hamulata* and the moss *Fontinalis antipyretica* occurred under conditions of elevated NO_3^- but reduced NH_4^+ levels in our study region. Other chemical factors such as the availability of basic cations (Ca^{2+}, K^+, Mg^{2+}) may be less influential for community composition in our study region, because weakly acidic waters with pH <7 in the water column and low conductivity and cation concentrations were lacking in our sample.

Conclusions

Current velocity in combination with the occurrence of characteristic macrophytic growth forms are the most promising parameters for categorizing the river and stream habitats of the north-west German Pleistocene. The rather low indicative value of chemical factors is partly a consequence of the dominant mechanical factors in running waters, but may also be caused by decades of anthropogenic interference, which must have greatly reduced former gradients in water and sediment chemistry as well as hydromorphology across the catchments. Despite some limitations, our study confirmed the indicative value of macrophytes for the abiotic and biotic conditions of streams and rivers as it has been found, e.g. for southern Germany (Poschlod et al. 2010) and other European countries (Birk and Willby 2010). This potential should be used for ecological quality assessment as required by the European Water Framework Directive.

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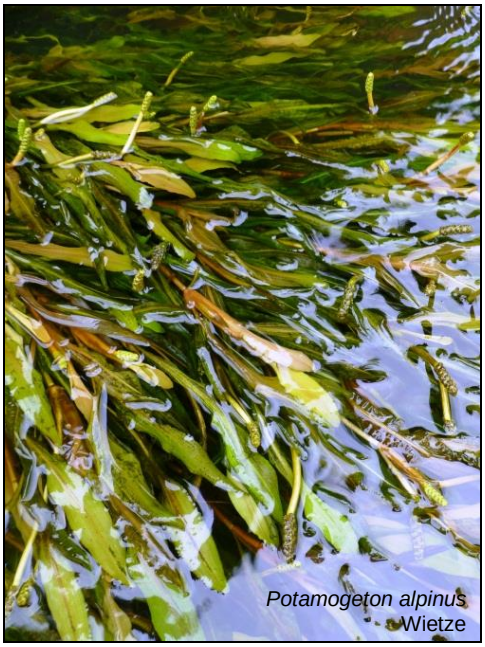
Chapter 3

Diversity loss in the macrophyte vegetation of north-west German streams and rivers between the 1950s and 2010

Kristina Steffen, Thomas Becker, Wolfgang Herr & Christoph Leuschner

(*Hydrobiologia* 2013, 713(1), 1–17)


Potamogeton alpinus, Wietze


Potamogeton perfoliatus, Behler Bach


Lemna minor and *Spirodela polyrhiza*, Kossau


Myriophyllum spicatum, Oker

Abstract

This resampling study in 338 semi-permanent plots analyses changes in river macrophyte diversity in 70 water courses (small streams to medium-sized rivers) from four regions of the north-west German lowlands during the last six decades. The total macrophyte species pool decreased between the 1950s and 2010/2011 by 27.5 % (from 51 to 37 species), mean plot-level species richness by 19.4 % (from 4.7 to 3.8 species per relevé) and the number of red-listed species by 40.0 % (from 30 to 18 species). Species loss was associated with marked change in species traits: species with presumably higher mechanical stress tolerance (indicated by low specific leaf area and short leaf longevity) are more abundant today. Nearly half of the species present in the 1950s had either disappeared or been replaced by other species in the recent relevés. The dramatic impoverishment is likely a consequence of continued nutrient input that drove oligo- and mesotraphent species to extinction, and of restructuring and maintenance works in the water courses that reduced stagnant and undisturbed river habitats, where stress-intolerant species can persist. Efficient measures to reduce the nutrient load and to re-naturalize stream and river beds are urgently needed to halt and reverse the loss of macrophyte diversity.

Keywords: Aquatic macrophytes, eutrophication, running waters, species traits, vegetation change

Introduction

With less than 100 species, the hydrophytic macrophyte flora (Charophyta, Bryophyta, Pteridophyta and Spermatophyta) of Central Europe's running waters is relatively species-poor (Casper & Krausch 1981), but rich in different growth forms reflecting the considerable diversity of habitat types being present in streams and rivers of variable sizes, current velocities, water chemistries and sediment types. With rapidly increasing amounts of fertilizers used in the agricultural landscape and manifold hydro-engineering measures completed, the biota of running waters have been exposed to an ever-increasing pressure in the last century with consequences for macrophyte diversity and community composition (Phillips et al. 1978, Robach et al. 1996, Smith et al. 1999, Egertson et al. 2004, Hilton et al. 2006, Kozlowski & Vallelian 2009). Eutrophication of water bodies by oxidized and reduced nitrogen compounds, but also by phosphorus, is known to cause profound shifts in the plant community composition of running waters, where rooted macrophytes may eventually be replaced by green macroalgae or phytoplankton as a consequence of light deficiency (Sand-Jensen & Borum 1991, Vadineanu et al. 1992, Marques et al. 2003).

Aquatic macrophytes have frequently been used in limnology and vegetation ecology as reliable indicators of habitat conditions in running waters, because various species respond sensitively to alteration in water chemistry and/or current velocity (Kohler & Schneider 2003, Schaumburg et al. 2004, Daniel et al. 2006, Demars & Trémolières 2009). As an outcome of macrophyte monitoring, plenty of information exists on the ecological conditions of streams and rivers in many European regions (Pott 1980, Wiegleb 1981, Riis et al. 2000, Kuhar et al. 2007, Grinberga 2011). However, this information is predominantly of qualitative nature and does not provide reliable information on long-term changes in the diversity and composition of the vegetation or alteration in environmental conditions that affect community composition. Only a limited number of studies on long-term change in river macrophyte communities covering several decades exists (Whitton & Dalpra 1967, Holmes & Whitton 1977, Herr et al. 1989, Mesters 1995, Whitton et al. 1998, Riis & Sand-Jensen 2001, Schwieger 2002, Schütz et al. 2008) and an over-regional picture of diversity loss has not yet emerged.

This study uses a semi-permanent plot approach to analyse long-term change in the macrophyte vegetation of 70 streams and rivers from four regions in north-west Germany from the mid of the 20th century until present. We resampled 338 relevés taken between 1936 and 1969 in 2010/2011 and analysed changes in species diversity, abundances of growth forms and functional traits at the community level including specific leaf area (SLA) and the indicator value for nitrogen. For a restricted data set, the temporal development of community change could be analysed between the 1950s, the 1980s and present. The aim of our study was to examine long-term changes in stream and river macrophyte vegetation from an over-regional perspective and, in case of changes, to elucidate the possible drivers of change. More specifically, we asked (1) if the decrease in macrophyte species richness among the 1950s and 2010/2011 was a general phenomenon in all studied river systems, (2) if nutrient-demanding and stress-tolerant species increased proportionally and (3) if community change has been more profound between the 1950s and the 1980s than between the 1980s and 2010/2011.

Materials and methods

Study area

Four regions located in the Pleistocene north-west German lowlands with a variety of small streams to medium-sized rivers were selected for study. Region 1 comprising the Ems-Hunte moraine (mainly Dümmer lowlands) with acid base-poor moraine soils and bogs; region 2, the Lüneburg Heath (including the Aller lowlands) with base-poor sandy soils, both formed by the penultimate (Saale) Ice Age; region 3, (a) the northern Harz foothills with fertile Pleistocene loess deposits and (b) running waters at the base of the Weser-Leine uplands; and region 4, the eastern Holstein moraine with more base-rich young moraine soils of the

last (Weichsel) Ice Age (Figure 3.1). Region 3 combines the subregions (a) and (b), because all those sites are situated at the southern edge of the north German Pleistocene lowlands where runoff and groundwater are influenced by the silicate- or carbonate-rich bedrock of the uplands. In total, 70 rivers and streams were sampled (Table 3.1 in the Appendix) covering a broad range of water courses with small to medium size (1–40 m width and 0.2–2 m depth), current velocities between 0 and 50 cm s^{-1} and sandy or loamy sediments partly overlain by organic deposits or gravel. The catchments of all rivers are part of the cultural landscape of north-west Germany, consisting of a mosaic of arable fields, pastures, meadows, forests and settlements. While the river sediments of the regions 1 and 2 are base-poor and those of the regions 3 and 4 moderately base-rich, in the last decades all streams and rivers have received considerable nutrient loads from the adjacent intensively managed agricultural land (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit 2010). Due to the oceanic influence, the north-west German lowlands have a humid climate, characterized by warm summers and relatively mild winters with short frost periods. Mean annual temperatures range around 9 °C, with lowest mean temperatures in January (0.4 °C Braunschweig, Lower Saxony) and highest mean temperatures in July (17.2 °C Hannover, Lower Saxony). The average annual precipitation lies between 656 mm y^{-1} (Hannover) and 754 mm y^{-1} (Kiel, Schleswig-Holstein) (all climate data from Deutscher Wetterdienst 2012).

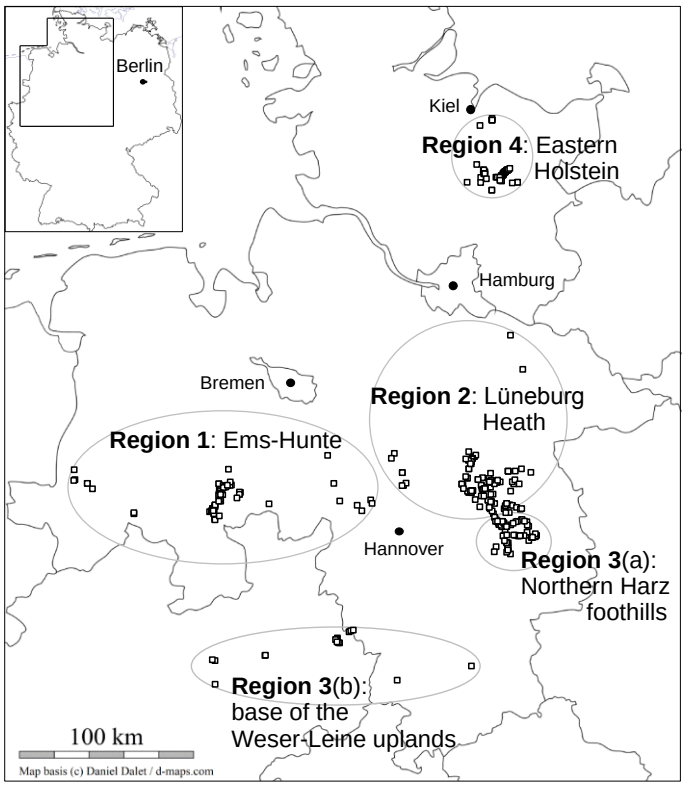


Figure 3.1 Location of the study sites (open squares) within four regions of north-west Germany: region 1 = Ems-Hunte moraine, region 2 = Lüneburg Heath (including the Aller lowlands), region 3 = (a) Northern Harz foothills and (b) parts of the Weser-Leine uplands and region 4 = Eastern Holstein moraine

Data basis

We analysed data sets from three different periods (A: 1936–1969, B: 1983–1986, C: 2010/2011). Set A, referred to as the 1950s data, contains 338 relevés from the literature (Roll 1939, Weber-Oldecop 1969) and from the Reinhold-Tüxen-Archive in Hannover (Hoppe 2005). The relevés deposited in the Tüxen archive were mostly taken by Rudolph Alpers in 1946. Set B contains 100 relevés from the 1980s of locations that were all sampled in the periods A and C (Herr & Wiegleb 1984, Herr 1987). Set C contains present-day data of 338 locations congruent with set A. In the analysis, we first compared the data sets A (1950s) and C (2010/2011) (two-step comparison); in a second step, subsets of these two sets were compared with data set B (1980s), because only 100 sites were available that had been sampled in the 1950s, the 1980s and 2010/2011 (three-step comparison). The second analysis examined the time course of community change in more detail and the results are presented in the "Results" section ("Time course of community change: comparing the 1950s, the 1980s and 2010/2011"). Subset AϵB contains those data of set A that relate to the 100 locations of set B and subset CϵB includes the data of set C that refer to the 100 locations of set B. The plot sizes of the recent relevés (set C) were chosen in correspondence with the plot sizes of set A (varying between 1 and 100 m²). If no plot size was indicated in the historical relevés, a size of 40 m² was sampled, which is the average of all indicated plot sizes in several hundred relevés from streams and rivers available at the Tüxen archive. No uniform plot size could be achieved in the three-step-comparison (see below under "Methodological restrictions").

Sampling design and field methods

Historical and recent vegetation analysis was conducted with the relevé method by determining all occurring plant species in a plot and estimating their cover either in percent or (in a few cases) in cover classes according to Braun-Blanquet (see Dierschke 1994). In order to repeat the historical relevés (set A), the original sampling sites as indicated in the historical sources were revisited in the vegetation periods (June to September) of the years 2010 and 2011. In the reach of a sampling location, we chose a site where the macrophyte vegetation was well developed, because a similar selection procedure had generally been adopted by the authors 60 years ago. Particularly species-poor stands (e.g. under shading trees or next to artificial structures) were not selected. Relevé size was adapted to the size of the respective historical relevé. In addition, a standard plot size of 100m² was sampled in 2010/2011 and used for the three-step-comparison. Vegetation was inspected using wade trousers and a telescopic rake was used in deep or very turbid water. The cover values of all macrophyte species that rooted in the river bed below the water level were recorded. In addition, several environmental parameters were recorded, notably the width and depth of

the water body, flow velocity (determined in the stream line with the drift method as it had been used by Weber-Oldecop, 1969) and the sediment type within the plot.

Data analysis

Cover values that were available in scores of the scales according to Braun-Blanquet (1964; non-decimal) or Londo (1976; decimal) were transcribed into percentage cover values for every species, using the mean percent value of the respective class. All cover values, including those having been estimated in percent, were then transcribed into the mean percent value of the corresponding Braun-Blanquet class, to obtain consistent scaling among the data sets. Diversity changes were quantified using a modification of Shannon's diversity index, i.e. true diversity D according to Jost (2006), with $D = e^{H'}$, where H' is Shannon's diversity index and D the number of species that would be needed to produce the given Shannon diversity value, if cover values were evenly distributed. For comparing the species composition of pairs of historical and recent relevés at a site, we calculated the dissimilarity index after Lennon (Lennon et al. 2001) with Lennon DI = min (b,c) / [min (b,c) + a], where a is the number of species being present in both relevés, b the number of species only occurring in relevé 1 and c the number of species only occurring in relevé 2. In contrast to other indices of species turnover, the Lennon DI does not generate high dissimilarities from high differences in species richness, but concentrates on compositional differences with values between 0 (a relevé includes all species of the other relevé) and 1 (no species in common). The current red list of endangered ferns and flowering plants of Germany (Korneck et al. 1996) was used to identify endangered macrophyte species (see Table 3.2 in the Appendix). Plant growth forms were determined after Segal (1968), Mäkirinta (1978) and Wiegleb (1991). Information on pollination types was taken from the BiolFlor data base (Klotz et al. 2002) and on SLA from the LEDA database (Kleyer et al. 2008). The strategy type classification (CRS-system) follows Landolt et al. (2010). Information on leaf longevity and on the species' ecological indicator values for temperature, nitrogen and soil reaction were taken from Ellenberg et al. (2001). The Ellenberg indicator values (EIVs), which are based on vast expert knowledge about the species, have repeatedly been proven for reliably characterizing the environmental conditions of Central European plant communities (Hill et al. 2000, Diekmann 2003, Jansson et al. 2007). They were available for all species occurring in the analysis except for the two aggregates. To facilitate the analyses, similar plant functional groups were aggregated: the pleustophyte group includes lemnids, ricciellids, ceratophyllids and hydrocharids; the potamids contain parvo- and magnopotamids. The group of zoogamous species contains all species pollinated by insects and/or snails. With respect to leaf longevity, only two categories (evergreen and summergreen) were distinguished and the analyses were run with the percental proportion of evergreens.

All statistical tests and correlation analyses were done with the package SPSS 15.0 (SPSS Inc., Chicago, USA). When two time steps (1950s vs. 2010/2011) were compared and values were normally distributed (according to a Shapiro-Wilk test), the t-test for paired samples was used to test for significance. For data that were not normally distributed and could not be transformed, the non-parametric Wilcoxon-test was used. When three time steps (1950s vs. 1980s vs. 2010/2011) were compared, a repeated measures ANOVA was used to test for differences. In cases, where an overall effect was found, the differences between the groups were further tested with the Bonferroni post hoc test. The species richness estimator indices ACE, ICE, Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap and MMmeans were calculated from species presence/absence matrices with the software EstimeS 8.20. An indicator species analysis (ISA) after Dufrêne & Legendre (1997), where indicator values are generated from a combination of a species' frequency and abundance in a particular group, was carried out with PCOrd 5.1. ISA analyses comparing historical and recent samples were performed for each of the four study regions separately and also for the pooled data set across all regions. The indicator values were tested for significance using Monte Carlo randomizations with 9999 permutations (Bakker 2008). A detrended correspondence analysis (DCA) (Hill & Gauch 1980) was done with Canoco 4.56, where information on environmental and biological traits was correlated with the DCA axes in a post hoc manner. Traits were calculated for each relevé as means (EIVs, SLA) or proportions (growth forms, strategy types, leaf longevity) to be fitted on the ordination space in the form of arrows pointing into the direction in which the value of the variable increases (Leps & Smilauer 2003). For variables that were not normally distributed we used Spearman correlation, for normally distributed variables Pearson correlation. The respective types of correlation analysis are listed in Table 3.3 in the Appendix.

Methodological restrictions

To achieve sufficient comparability among the different data sets, only hydrophytic species (plants with morphological adaptations to life in water in the form of submerged or floating leaves) were included in the analyses. Amphiphytes and terrestrial plants, which may have been present in certain relevés when taken at high water, were excluded, because these species were not treated uniformly by the different authors. In the three-step-comparison (time course analysis), relevés of different sizes had to be compared. The 1950s relevés (subset AϵB) had the smallest size, the 1980s relevés (set B) were largest and the 2010/2011 relevés (subset CϵB) were intermediate in size. It thus can be assumed that the species richness in the 1950s may have been rather underestimated, especially when compared to the richness in the 1980s. Despite these methodological shortcomings, it is probable that the species pool of each region was adequately characterized in our analysis

even with the relatively small relevés of the 1950s, as most water courses were sampled at several sites (see also Figure 3.4).

The reliability of species identification in historical time was not always sufficient. In case of two genera with difficult species determination, aggregates were used throughout the analyses: the species *Callitriche cophocarpa* Sendtner, *C. obtusangula* Le Gall de Kerlinou, *C. palustris* Linnaeus, *C. platycarpa* Kützing, *C. stagnalis* Scopoli and *C.* x *vigens* Martinsson were summarized to *C. palustris* agg. and the species *Ranunculus aquatilis* L. and *R. peltatus* von Schrank were summarized to *R. aquatilis* agg. In the text, aggregates and hybrids are referred to as species. The floristic knowledge of the historical author R. Alpers was assumed to be very good; only the fact that he mistook *Potamogeton natans* L. for *P. nodosus* Poiret (based on his own notes as cited in Herr et al. 1989) was taken into account by correcting for this mistake. Similarly, the species identifications of D.W. Weber-Oldecop were considered to be reliable throughout. Regarding the earliest historical author H. Roll, who worked in region 4 (eastern Holstein), it astonishes that the common macrophyte *Sparganium emersum* Rehmann did not appear in his species lists. As taxonomical literature was not sufficiently developed in his time, he might have confused this species with *Glyceria fluitans* (L.) Brown (Weber-Oldecop 1982) or *Sparganium erectum* L.; however, we did not change any identification into *Sparganium emersum* in Roll's data for not increasing possible errors.

Results

Change in floristic composition and diversity between the 1950s and 2010/2011

In all 676 historical and recent relevés covered by the analysis, 55 hydrophytic macrophyte species were recorded. The number of macrophyte species dropped by 27.5 % from 51 species in the 1950s to 37 species in 2010/2011. Four species [*Elodea nuttallii* (Blanchon) St. John, *Potamogeton praelongus* von Wulfen, *P. trichoides* von Chamisso & von Schlechtendal and *Wolffia arrhiza* (L.) Wimmer] were recorded in the recent, but not in the historical survey. On the other hand, 18 species [*Helosciadium inundatum* (L.) Koch, *Hippuris vulgaris* L., *Juncus bulbosus* L., *Leptodictyum riparium* (Hedwig) Warnstorf, *Luronium natans* (L.) Rafinesque, *Nymphaea alba* L., *Potamogeton acutifolius* Roemer & Schultes, *P. alpinus* Balbis, *P. angustifolius* Presl, *P. compressus* L., *P. filiformis* Persoon, *P. friesii* Ruprecht, *P. gramineus* L., *P. obtusifolius* Mertens & Koch, *P. polygonifolius* Pourret de Figeac, *Ranunculus circinatus* Sibthorp, *Sparganium natans* L. and *Utricularia australis* Brown] were present in the historical, but not in the recent 338 relevés. In region 1 (Ems-Hunte), the loss in species richness was largest (Table 3.4). Lennon´s pairwise dissimilarity between historical and present-day relevés was 0.46 indicating that 46 % of the species of an average relevé pair were different and 54 % of the species were identical. Highest

dissimilarity between historical and recent relevés (70 %) was observed in the Holstein region and lowest (36 %) in the Lüneburg Heath region. The number of red-listed species present in the study area dropped by 40 % from 30 in the 1950s to 18 in 2010/2011.

Table 3.4 Total number of species and red-listed species in the 1950s and in 2010/2011 and their proportional increase or decrease in the four study regions. The Lennon dissimilarity index describes the quantitative species turnover. The assignment of red-listed status refers to the species' current vulnerability status according to Korneck et al. (1996)

Region	No. of species 1950s	No. of species 2010 /2011	Change in no. of species [%]	No. of red-listed species 1950s	No. of red-listed species 2010/2011	Change in no. of red-listed species [%]	Lennon's dissimi-larity
All regions	51	37	-27. 5	30	18	-40.0	0.46
Ems-Hunte	37	25	-32.4	20	9	-55.0	0.49
Lüneburg Heath	31	23	-25.8	14	7	-50.0	0.36
Harz foothills	27	25	-7.4	10	8	-20.0	0.40
Holstein	19	17	-10.5	11	4	-63.6	0.70

The mean number of species per relevé decreased from 4.7 to 3.8 between the 1950s and 2010/2011 (Figure 3.2, Table 3.5 in the Appendix). Simultaneously, the percentage of red-listed species per relevé dropped from 20.4% to 8.6%, indicating a disproportionately larger decrease in this group. Diversity (true diversity D) declined from 2.8 to 2.3 in the whole sample. The indicator species analysis revealed 28 species (51% of the total species pool) to be suitable indicators in at least one region for either recent or historical relevés; in other words, the 28 species showed either a significant decrease or an increase in at least one of the regions (Table 3.6). Twenty-three species showed a decrease or increase between the 1950s and 2010/2011 that was significant in the whole sample and thus independent from the region. Within the species, the direction of change was highly consistent, i.e. nearly all species either increased or decreased in the four regions. However, 77 % of the species with a significant frequency change decreased or increased in only one or two of the four regions pointing to a large regional influence on community change. Only three species (*Nuphar lutea* (L.), *Potamogeton perfoliatus* L., *Ranunculus aquatilis* agg.) showed a decrease in three of the four regions, only one species *(Elodea nuttallii)* an increase in three regions. The only species, which decreased in all four regions, was the Canadian Waterweed, *Elodea canadensis* Michaux*,* which thus served as a highly reliable indicator for running waters of the 1950s. The four regions differed considerably with respect to the number of decreased species. In region 3 (Harz foothills), 15 species decreased, in region 2 (Lüneburg Heath) 13, in region 1 (Ems-Hunte) ten, and in region 4 (eastern Holstein) three. The numbers of species with frequency increase ranged from one to three in the regions. The ratio of

decreased to increased species was highest in region 2 (ratio of 6.5) followed by region 3 (5.0), region 1 (3.3) and region 4 (3.0), indicating that the losses in species frequency and abundance were high in the Lüneburg Heath and comparably low in the Ems-Hunte region and in eastern Holstein. In all regions together, 21 species decreased and only 2 species increased.

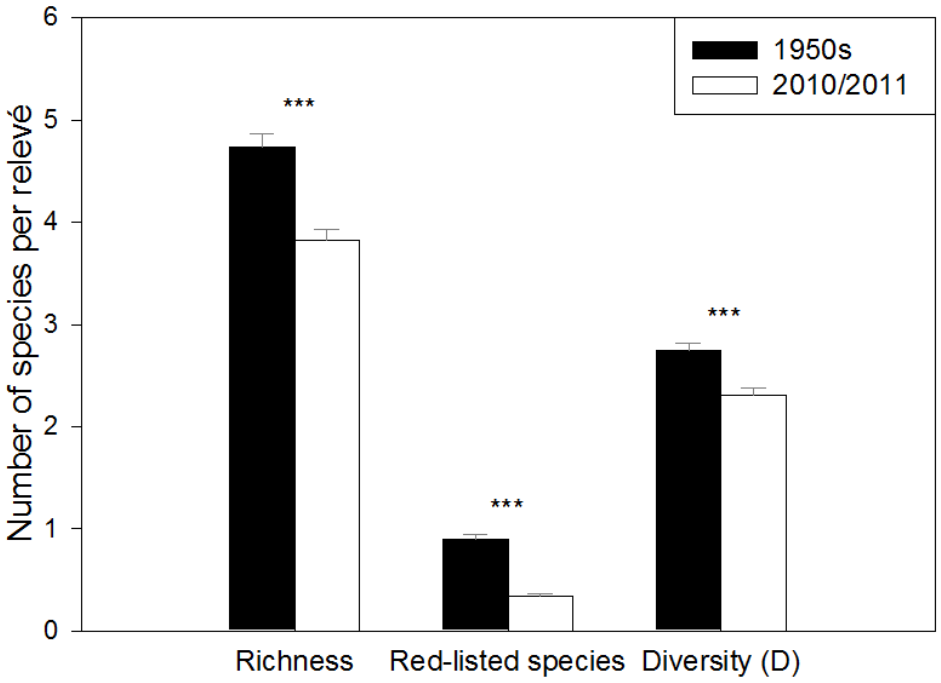


Figure 3.2 Species richness, number of red-listed species and diversity (true diversity D) per relevé in the 1950s and in 2010/2011 (means ± SE). Differences significant at p<0.001 are marked by ***. The assignment of red-listed status refers to the species' current vulnerability status according to Korneck et al. (1996)

Table 3.6 Macrophyte species of running waters which have increased or decreased in four north-west German regions between the 1950s and 2010/2011. Percent frequency (constancy) values are shown (historical relevés vs. recent relevés). Arrows indicate the direction of change: ↑ = increase, ↓ = decrease. The statistics base on the indicator species analysis; only species which have significantly (at p<0.1) decreased or increased at least in one region are listed

	All regions	**Region 1 (Ems-Hunte)**	**Region 2 (Lüneburg Heath)**	**Region 3 (Harz foothills)**	**Region 4 (eastern Holstein)**
Decreased species					
Callitriche hamulata	↓23.1→12.1***	n.s.	↓67.6→28.7***	n.s.	n.s.
Callitriche palustris agg.	↓41.4→32.0***	n.s.	↓63.9→47.2**	↓56.0→18.7***	n.s.
Ceratophyllum demersum	n.s.	n.s.	n.s.	↓9.9→3.3+	n.s.
Elodea canadensis	↓39.9→20.4***	↓35.9→32.1**	↓52.8→26.9***	↓20.9→3.3***	↓50.8→19.7***
Fontinalis antipyretica (moss)	↓6.8→3.3+	n.s.	↓14.8→1.9***	n.s.	n.s.
Juncus bulbosus fluitans	↓2.7→0.0**	n.s.	↓8.3→0.0**	n.s.	n.s.
Lemna minor	n.s.	n.s.	n.s.	↓52.7→33.0**	n.s.
Lemna trisulca	↓15.1→9.5**	↓26.9→21.8*	↓13.2→1.1**	n.s.	n.s.
Leptodictyum riparium (moss)	↓5.9→0.0***	n.s.	↓13.0→0.0***	↓6.6→0.0*	n.s.
Myriophyllum alterniflorum	↓9.5→4.4***	n.s.	↓28.7→13.0***	n.s.	n.s.
Nuphar lutea	↓34.6→24.0***	↓62.8→51.3**	n.s.	↓24.2→18.7*	↓32.8→11.5***
Potamogeton alpinus	↓5.3→0.0***	n.s.	↓13.9→0.0***	n.s.	n.s.
Potamogeton crispus	↓18.3→7.4***	↓16.7→6.4*	n.s.	↓42.9→17.6***	n.s.
Potamogeton friesii	↓9.5→0.0***	n.s.	n.s.	↓27.5→0.0***	n.s.
Potamogeton lucens	↓10.9→3.0***	↓26.9→9.0***	n.s.	n.s.	↓24.6→0.0***
Potamogeton natans	↓30.5→10.4***	↓62.8→26.9***	n.s.	↓39.6→2.2***	n.s.
Potamogeton obtusifolius	↓1.5→0.0+	n.s.	n.s.	n.s.	n.s.
Potamogeton pectinatus	↓16.0→10.4**	↓12.8→5.1*	n.s.	↓37.4→28.6*	n.s.
Potamogeton perfoliatus	↓12.4→3.0**	↓21.8→3.8***	↓9.3→1.9*	↓6.6→2.2+	n.s.
Potamogeton pusillus	↓6.8→3.6**	n.s.	n.s.	↓15.4→0.0***	n.s.
Ranunculus aquatilis agg.	↓23.4→8.0***	↓9.0→2.6+	↓59.3→23.1***	↓8.8→0.0**	n.s.
Ranunculus fluitans	↓4.7→2.4*	n.s.	n.s.	n.s.	n.s.
Sparganium emersum	↓52.1→52.1***	↓41.0→33.3*	↓79.6→78.7+	↓63.7→50.5***	↑0.0→31.1***
Increased species					
Elodea nuttallii	↑0.0→19.8***	↑0.0→41.0***	↑0.0→26.9***	↑0.0→6.6*	n.s.
Lemna gibba	n.s.	↑2.6→17.9***	↑2.8→9.3**	↓20.9→6.6**	n.s.
Myriophyllum spicatum	↑0.9→5.6***	n.s.	n.s.	↑1.1→17.6***	n.s.
Spirodela polyrhiza	n.s.	↑21.8→59.0+	n.s.	↑2.2→9.9*	n.s.
Species without overall increase or decrease					
Chiloscyphus polyanthos (liverwort)	n.s.	n.s.	↓4.6→0.0+	↑0.0→5.5+	n.s.
Numbers of decreased / increased species	21/2	10/3	13/2	15/3	3/1

n.s. = non-significant, + = p<0.1, * = p<0.05, ** = p<0.01, *** = p<0.00

Change in vegetation structure and biological traits between the 1950s and 2010/2011

The pleustophytic growth form types as well as vallisnerids increased in relative abundance from the 1950s to 2010/2011. In contrast, peplids, potamids, batrachids and nymphaeids declined. Isoetids disappeared completely (Figure 3.3, Table 3.7 in the Appendix). Competitor-strategists proportionally declined, while ruderal- and stress-strategists increased. The abiotic pollination types anemogamy and hydrogamy declined in the study area, while the relative frequency of self-pollinated macrophyte species and species pollinated by insects or snails increased. Species with evergreen leaves showed a decline, while the proportion of summergreen (short-lived) species increased. Species with a high specific leaf area, i.e. with leaves and lamina rich in aerenchymatic tissue, proportionally declined from the 1950s to 2010/2011 (Table 3.8).

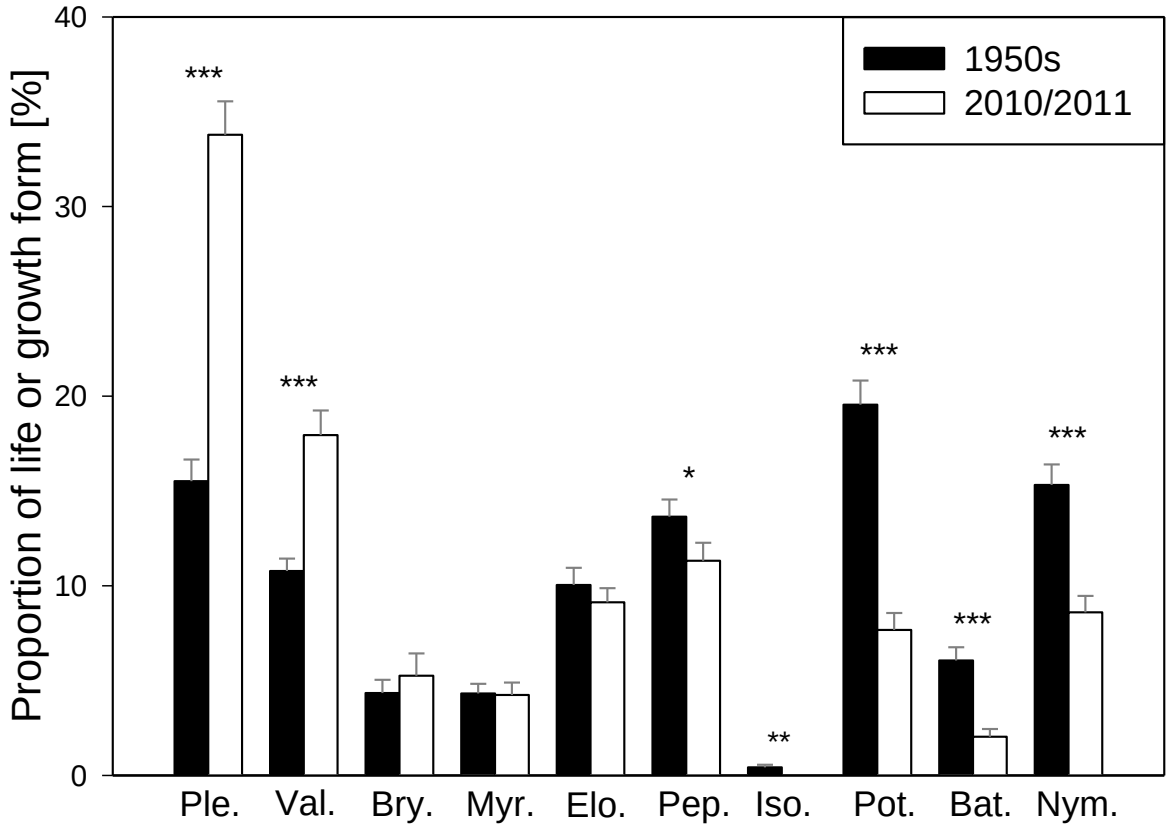


Figure 3.3 Proportions of the different growth forms in the total number of species in the relevés of the 1950s and 2010/2011 (means ± SE of 338 relevés); Ple. = pleustophytes (lemnids, ricciellids, ceratophyllids, hydrocharids), Val. = vallisnerids, Bry. = bryids, Myr. = myriophyllids, Elo. = elodeids, Pep. = peplids, Iso. = isoetids, Pot. = parvo- and magnopotamids, Bat. = batrachids, Nym. = nymphaeids. Significant differences are indicated (*** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$)

Table 3.8 Relative abundance of life strategies (CRS-classification), pollination types, leaf properties and mean Ellenberg indicator values among the species of the relevés from the 1950s and from 2010/2011. Mean values are shown

Trait	1950s	2010/ 2011	Direction of change[1]	T (paired t-test) / Z (Wilcoxon test)	p
C-strategists [%]	23.9	18.9	↓	T=5.9	<0.001
R-strategists [%]	11.2	14.5	↑	Z=-4.2	<0.001
S-strategists [%]	64.9	66.6	↑	Z=-4.2	<0.001
Anemogamy [%]	43.5	40.6	↓	Z=-3.4	<0.001
Hydrogamy [%]	28.5	24.6	↓	Z=-2.1	0.035
Autogamy [%]	10.2	11.3	↑	Z=-3.2	0.001
Zoogamy [%]	17.8	23.6	↑	Z=-4.7	<0.001
Evergreen species [%]	72.5	55.8	↓	Z=-7.5	<0.001
SLA [m^2 kg^{-1}]	37.9	29.4	↓	Z=-8.7	<0.001
EIV for temperature	5.5	5.5	↑	Z=-1.9	0.059
EIV for soil reaction	6.6	6.6	-	Z=-1.1	0.271
EIV for nitrogen	6.1	6.3	↑	Z=-5.8	<0.001

[1] ↓ = decrease, ↑ = increase

Change in environmental conditions between the 1950s and 2010/2011

The mean Ellenberg indicator values (EIV) for nitrogen and for temperature, calculated by averaging over all species of a relevé, have increased during the six decades of study (Table 3.8). No change was observed for the EIV for soil reaction (pH). Some major changes (significant at $p<0.001$) in river hydrography took place since the 1950s: Across all 70 water courses, we found an increase in the mean width of the water course (from 7.8 m to 10.1 m), an increase in mean water depth (from 0.8 m to 1.1 m), but an apparent decrease in mean current velocity in the stream line (from c. 0.30 m s^{-1} to c. 0.12 m s^{-1}). The relative abundance of the different sediment types (more than 50 % sand followed by gravel/stones, mud and loam in the order of decreasing frequency) remained relatively stable over time (Table 3.9). However, while all rivers were still flowing in their natural beds in the 1950s, reaches of the stream Bruchgraben and the river Grawiede (both region 1) have been restructured by cementation since then.

Table 3.9 Proportion of different sediment types in the 1950s and in 2010/2011 (145 sites, where information from the 1950s and 2010/2011 was available, are included)

Sediment type	Proportion in the 1950s [%]	Proportion in 2010/2011 [%]
Sand	55.18	58.12
Gravel / stones	22.30	19.77
Mud	13.45	15.75
Loam	6.78	3.47
Other (natural)	2.30	2.20
Other (artificial)	0.00	0.70
	100.00	100.00

Time course of community change: comparing the 1950s, the 1980s and 2010/2011

The detailed temporal analysis with 100 plots studied in the 1950s, the 1980s and at present showed over all regions a continuous decline in total vegetation cover in the relevés from 57 % in the 1950s to 43 % in the 1980s and to 28 % in 2010/2011. The absolute number of species present declined by 15% between the 1950s and the 1980s and by another 12% between the 1980s and 2010/2011. Comparison of the number of observed species with the estimated number of species according to species richness estimator indices confirms that our analysis captured the present species pool to a large extent in all three sampling periods (Figure 3.4). Despite the more or less continuous decrease in the over-regional macrophyte species pool size, the four regions followed individual patterns of change. A decrease between the 1950s and the 1980s in the total number of species present (–19 to 36 %) was recorded only in two of the regions (Ems-Hunte and Harz foothills) and none of the regions showed species pool declines of more than 6 % between the 1980s and 2010/2011 (Figure 3.5a). This pattern was different for the number of red-listed species with decreases of 17–59 % in two regions (Ems-Hunte and Holstein) between the 1950s and the 1980s and further decreases of 20–25 % in all regions except region 1 (Ems-Hunte) in the subsequent second time interval (Figure 3.5b). The change in species composition between the 1950s and the 1980s (42% of species exchanged) was more profound than the species turnover between the 1980s and 2010/2011 (37% of species exchanged).

Rhizophytes with floating leaves, represented by the growth form types nymphaeids and batrachids, declined between the 1950s and the 1980s, while potamids show a decline between the 1980s and 2010/2011. Pleustophytes increased between the 1980s and 2010/2011 (Figure 3.6, Table 3.10 in the Appendix). The relative abundance of species with a competitor strategy proportionally declined between the 1950s and 2010/2011 (Figure 3.7a, Table 3.10 in the Appendix). In contrast, stress-tolerating species increased in the sixty years, while species with a ruderal strategy increased between the 1950s and the 1980s. We found a shift from a high proportion of evergreen species to a high proportion of

summergreen species for the period from the 1980s to 2010/2011 (Figure 3.7b). The average specific leaf area (SLA) of the species declined from c. 37 to c. 29 m^2 kg^{-1} with a large drop since the 1980s (Figure 3.7c). The mean Ellenberg indicator value for nitrogen strongly increased between the 1950s and the 1980s, but showed a tendency to decrease thereafter (Figure 3.7d). The EIV for soil reaction showed a similar pattern with a peak in the 1980s.

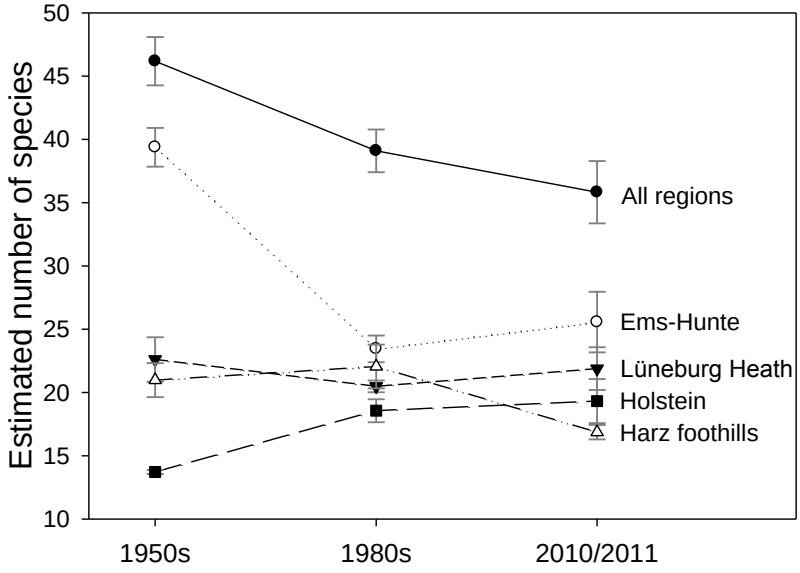


Figure 3.4 Estimated number of species for the 1950s, 1980s and 2010/2011, differentiated by regions. Mean values calculated from the species richness estimator indices ACE, ICE, Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap and MMmeans for data set B (1980s) and subsets AϵB (1950s) and CϵB (2010/2011). Given are the means and the average standard deviation over all relevés in a region

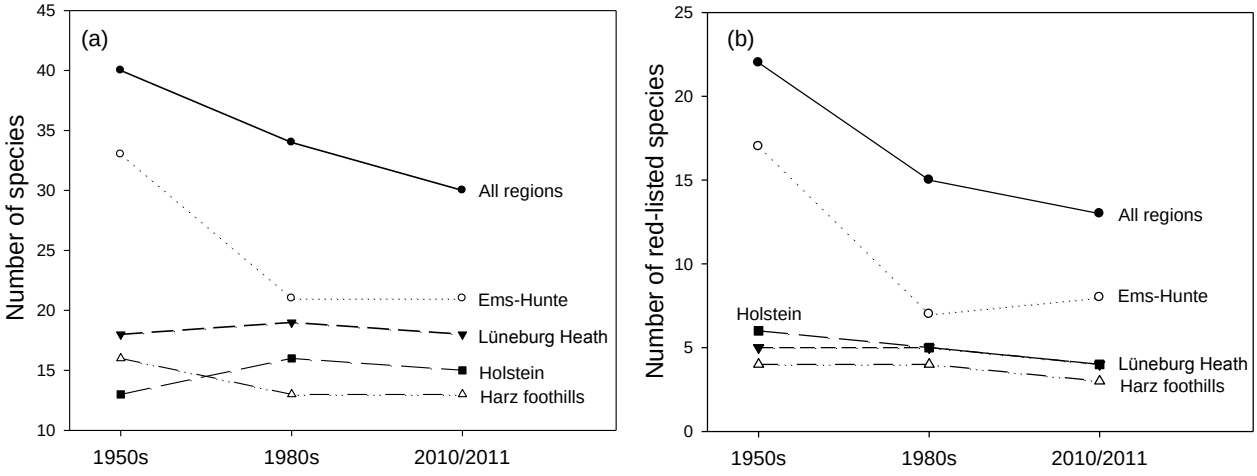


Figure 3.5 Total number of species present (a) and number of red-listed species present (b) in the 1950s, 1980s and in 2010/2011(data sets AϵB, B and CϵB), differentiated by regions

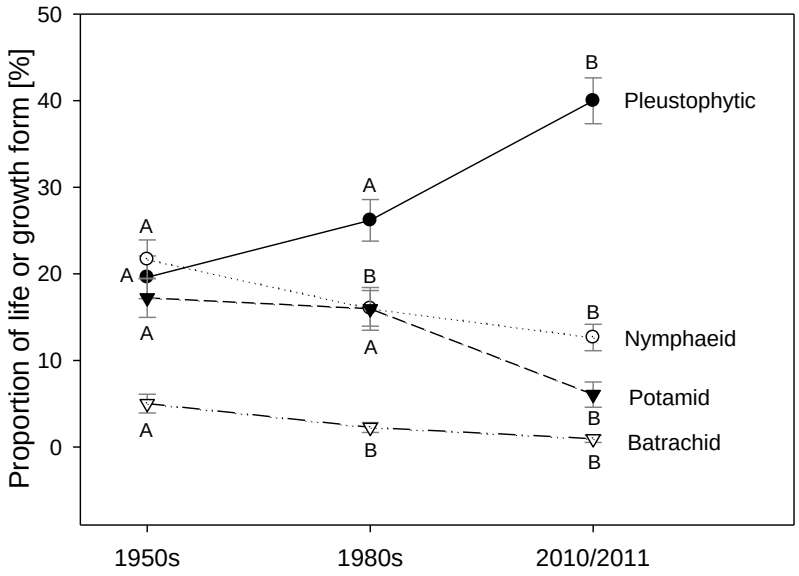


Figure 3.6 Proportions of pleustophytic (lemnid, ricciellid, ceratophyllid and hydrocharid) and rhizophytic (nymphaeid, potamid and batrachid) growth form types in the total number of species present in the 1950s, 1980s and 2010/2011 (means ± SE of 100 relevés). Different letters indicate significant differences between the sampling dates

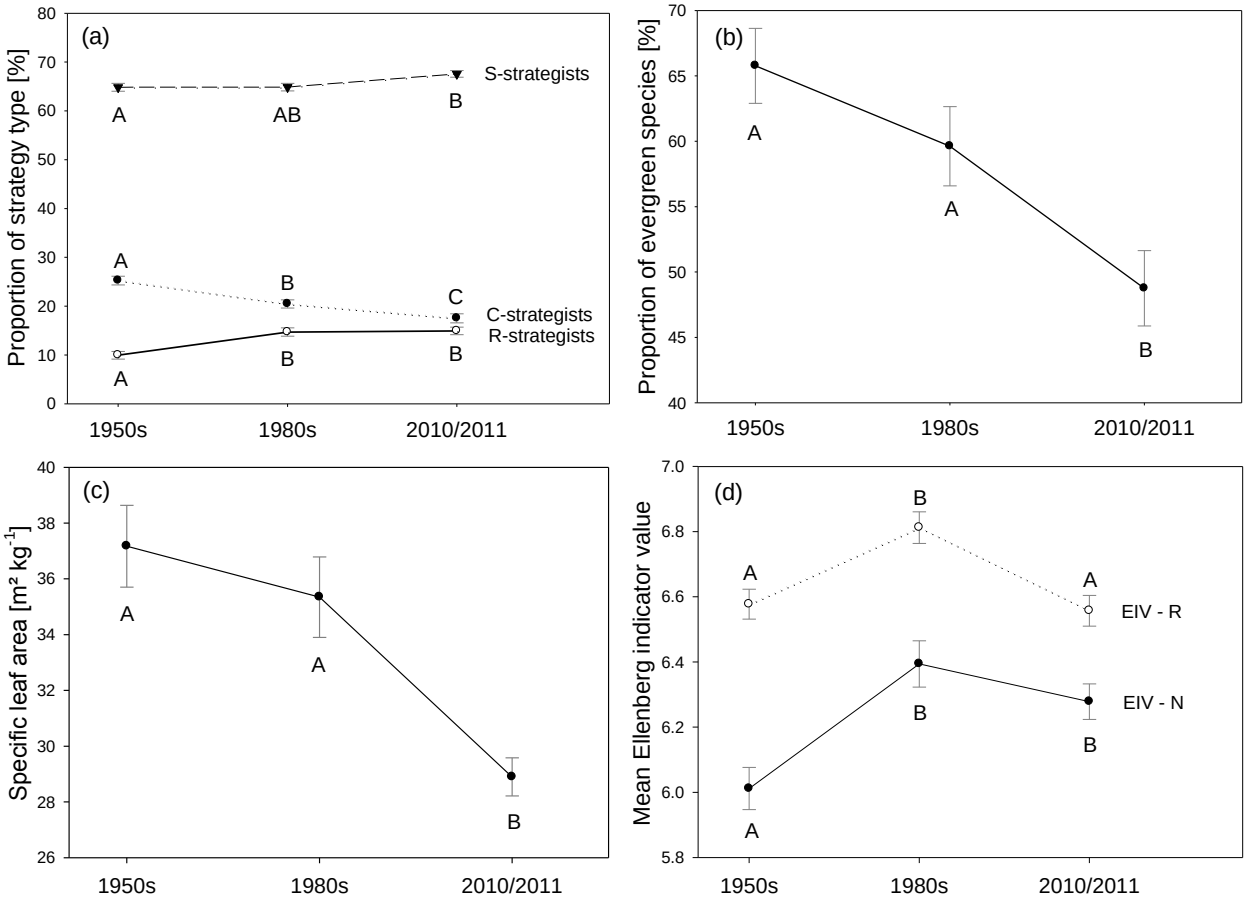


Figure 3.7 Mean relative proportion of (a) different plant strategy types, (b) evergreen species, (c) mean specific leaf area and (d) mean Ellenberg indicator values for nitrogen and soil reaction in the 1950s, 1980s and 2010/2011. Means and standard errors are given (n=100 relevés)

The DCA analysis, based on 284 relevés of 100 locations that were sampled three times (in the 1950s, the 1980s and 2010/2011), revealed two main axes (eigenvalues 0.607 and 0.455) with the first axis sharing a close positive correlation with current velocity and a negative correlation with the EIVs for soil reaction (pH) and temperature (Figure 3.8, Table 3.3 in the Appendix). Further, the relative abundance of competitors and of batrachid species correlated positively with axis 1, while this axis showed negative correlations with the relative abundance of stress tolerators and pleustophytic species. The second axis correlated positively with time (i.e. the year of sampling) and the relative abundance of pleustophytes, and negatively with SLA, the number of red-listed species per relevé and the relative abundance of potamids.

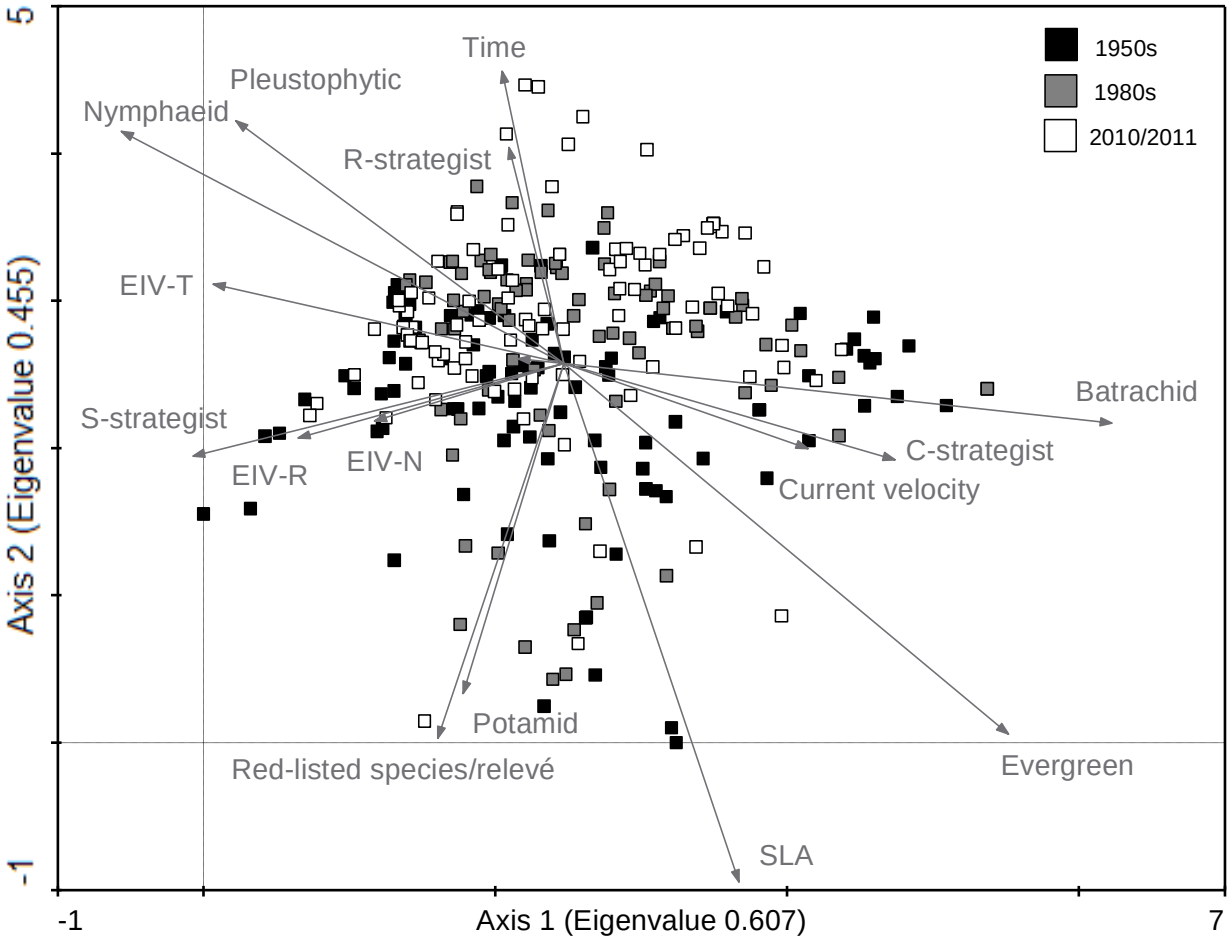


Figure 3.8 DCA graph based on 100 relevés from the 1950s resampled in the 1980s and 2010/2011 together with data (plot-level means) on the abundance of red-listed species, specific leaf area (SLA), proportion of evergreen species and plant life / growth forms, strategy type abundance, Ellenberg indicator values (EIVs) for nitrogen, temperature and soil reaction, and current velocity. For the ordination, species abundances were log-transformed and rare species were down-weighted; 15 relevés that did not contain macrophytes in recent time and one outlier were excluded

Discussion

Our analysis of long-term vegetation change in 70 water courses of variable size, flow velocity and bedrock chemistry in an extended area of north-west Germany showed large reductions in the regional macrophyte species pool (-27.5 %) and in plot-level species richness (-19.4 %) during the past 60 years or so. The loss in the number of currently red-listed species (-40.0 %) in the regional species pool was even larger indicating that species with specific habitat requirements, which are usually more threatened by habitat change than generalist species, were indeed most vulnerable. Species loss was related to marked changes in macrophyte community composition with nearly half of the species present in the relevés in the 1950s either having disappeared until 2010/2011 or having been replaced by other species. The current macrophyte communities are not only species-poorer, but also consist of species with higher mechanical stress tolerance as indicated by a reduced specific leaf area and shorter leaf duration. A large increase in the relative importance of pleustophytic species at the expense of potamid and nymphaeid species reflects the profound alteration in community structure during the past 60 years.

A more detailed analysis showed that species loss and community change occurred more or less continuously during the past six decades and may continue if no measures to halt biodiversity erosion are taken. However, we found large differences in the temporal evolution of vegetation change among the four studied regions, which reflect local developments in hydro-engineering and, likely, also in agricultural intensification. The diversity decline in the macrophyte vegetation of north-west German lowland water courses over six decades has to be attributed to a variety of causes. Increased nutrient inputs with the intensification of agriculture since the 1950s have accelerated the eutrophication of most freshwater habitats (Ellenberg & Leuschner 2010). The loss of species with preference for oligotrophic waters in our study area, such as *Helosciadium inundatum*, *Juncus bulbosus*, *Luronium natans*, *Potamogeton filiformis*, *P. polygonifolius*, *Sparganium natans* or *Utricularia australis*, is most likely a direct consequence of eutrophication. The increase in the mean Ellenberg indicator value for nitrogen from c. 6.0 to 6.4 between the 1950s and the 1980s reflects increased nutrient availability in the water courses. Furthermore, the increase in the pleustophytic species *Ceratophyllum demersum*, *Lemna* spp. and *Spirodela polyrhiza* is also most likely a consequence of eutrophication. Apart from these species being competitive in exploiting nutrients, their free-floating growth forms allow them to remain on or close to the water surface, where they can escape light limitation in phytoplankton-rich, turbid water. *Ceratophyllum demersum* is able to relocate its biomass into the uppermost water layer (canopy forming) under turbid water conditions (Garniel 2008). Our results are in line with findings from streams in the Netherlands, where Mesters (1995) reported a shift from submerged to floating-leaved species over several decades, which he explained with

increased water turbidity, because floating-leaved and emergent species do not depend on light transmission in clear water.

Potamal rivers are generally more affected by the influx of nutrient-enriched surface water from adjacent lands than rhithral water courses, because river water accumulates nutrients, while flowing through a catchment area with predominant agricultural land use. In fact, the changes in species composition were least pronounced in the groundwater-fed water courses of the Lüneburg Heath, which mostly have a rhithral character. While most rhithral streams are located in mountainous terrain, a number of running waters in the Lüneburg Heath region (region 2) are relatively cool in summer, due to groundwater inflow and thus also have rhithral characteristics, despite being located in the lowlands. In contrast, a comparatively high species turnover was found in the regions Ems-Hunte and eastern Holstein, where potamal rivers prevail in the intensively used agricultural landscape. With the embankment of the Dümmer lake and its main tributary Hunte river in 1953, the Dümmer lowlands, where the majority of sites in the Ems-Hunte region is located, have been transformed from a landscape dominated by swamps and fens to an area, where arable land is predominant and high nutrient inputs are affecting the wetland vegetation (Blüml et al. 2008). This regional development explains the huge loss of diversity in the Ems-Hunte region, where some effluents of the Dümmer lake have already reached the hypertrophic state (Niedersächsisches Landesamt für Ökologie 2001).

Since the 1980s, some improvement in the nutrient status of the running waters of north-west Germany has occurred. The slight decrease in the mean EIV for nitrogen, as observed since the 1980s, might reflect a decreased mineral nitrogen load in the studied river systems. The most important pathway of nitrogen into the water courses is runoff from agricultural lands, which accounts for about two thirds of total input. This diffuse fraction remained relatively stable, while inputs from point sources could be substantially reduced between 1983 and 2005 (German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety & German Federal Ministry of Food, Agriculture and Consumer Protection 2008). The input of phosphorus to surface waters has significantly decreased in the study area between 1980 and 1996, mainly as a consequence of reduced phosphorus contents in detergents and better sewage treatment (Schulz 1999). It appears that the vegetation is responding only slowly to these achievements.

In consideration of the previously discussed eutrophication effects, our finding of a decline in the floating-leaved growth forms nymphaeids and batrachids is somewhat perplexing. However, apart from eutrophication effects, the loss in structural diversity of river beds is another complex of factors responsible for the macrophyte diversity decline in rivers and streams in Central Europe (Wiegleb et al. 1991). Looking at the respective species in detail, it becomes obvious that the nymphaeids *Luronium natans* and *Nymphaea alba* and the

batrachids *Potamogeton gramineus* and *P. polygonifolius* as well as a myriophyllid species that disappeared, *Ranunculus circinatus*, are bound to habitats where the water is constantly stagnant to slowly flowing (Casper & Krausch 1980, 1981). Due to the anthropogenic reduction in structural diversity especially in lowland water courses, areas protected from the current, like inlets and shallow sections in the transition zone to floodplains, have become rare since the 1950s (Kaiser 1993, Rasper 2001). In 2000, 85% of all river beds in the northern German federal state of Lower Saxony were in the state of having a substantially modified, unnatural morphological structure (Niedersächsisches Landesamt für Ökologie 2001). With the aim to speed-up runoff and increase landscape drainage, many river beds were deepened and broadened and the river course straightened, resulting in the loss of retention areas and in an overall decrease in mean current velocity in the potamal rivers. These melioration measures were supplemented by stabilization works on the river beds conducted in Lower Saxony particularly between the 1950s and the 1980s (Wasserverbandstag e.V. 2011). In regulated lowland rivers, straightened and steep banks are limiting macrophyte growth (Lorenz et al. 2012). In addition, most of the studied lowland water courses are continuously maintained and hence subject to regular disturbance (Federal Water Act of Germany 2009).

It is thus not surprising that stress-tolerant species make up the largest proportion of the macrophyte flora since the 1950s, which is interpreted as a sign that most water courses had lost their systems of dead channels and shallow side arms with its characteristic flora already decades ago. The proportional increase in the ruderal strategy type, which comprises species with a high reproduction rate and the ability of rapidly colonising open sediments, is a sign for irregular disturbance by maintenance works in the water courses (Trémolières 2004). The increase in species with a low specific leaf area may also indicate increased disturbance levels in recent time. In general, species with lower SLA and higher tissue density have a higher mechanical strength which facilitates survival in waters with higher flow velocity. We assume that in deepened and partly canalized water courses with temporarily high flow rates and a lack of retention areas, macrophytes with robust structure are favoured. We propose that the mean specific leaf area of a macrophyte community and its change over time may serve as a suitable indicator of the hydromechanical stress that is imposed on the plants as a consequence of river construction works.

Half of the 18 species that have disappeared in the study area between the 1950s and 2010/2011 belong to the genus *Potamogeton*. A severe loss of *Potamogeton* species was also observed in Danish lakes and streams over the last 100 years and was related to low remaining habitat diversity and frequent disturbance in our times (Sand-Jensen et al. 2000). Our study confirms these findings, as only the fast-growing, disturbance-tolerant pondweeds *Potamogeton crispus*, *P. natans* and *P. pectinatus* are still relatively common in north-west

Germany. Nevertheless, the frequencies of these species have also decreased since the 1950s to 60–30 % of their former values. As most *Potamogeton* species are pollinated by water and wind, the decline in potamids resulted in a general decrease in hydrogamous and anemogamous species as well. Of the four species which have not been observed in the relevés before 2010/2011, *Elodea nuttallii* is a neophyte that was found in Germany for the first time near Münster (Westfalen) in 1953 and is now widespread (Starfinger & Kowarik 2003). *Potamogeton praelongus* has always been a rare species in the study area (Casper & Krausch 1980), while *P. trichoides* is a species considered vulnerable in Germany, where it has increased in the last decades (Haeupler & Muer 2000, Ludwig et al. 2007). The latter is not a typical species of running waters; it is considered to be relatively abundant in ponds, ditches and canals throughout its native range in Europe, Asia and Africa (Allen 2011).

Mean winter temperature in Lower Saxony has risen by 1.9 °C from 1950 to 2005 (Haberlandt et al. 2010). That summergreen species have experienced a relative increase, while evergreen species decreased, is probably mainly a consequence of increased disturbance intensity and not related to altered winter temperatures. Summergreens, overwintering with seeds or turions in the sediment, may be more tolerant to cold winters than evergreen macrophytes. Recent warming may have supported the arrival of *Wolffia arrhiza*, an indicator species for warm temperatures, in the study area in the last decades. Further warming may result in profound community change as is indicated by a modelling study for Finland, which predicts substantial changes in macrophyte community composition by 2050 with an increase in emergent macrophytes that may overgrow sensitive submerged macrophyte species (Alahuhta et al. 2011). Nevertheless, in the perspective of two to three decades, eutrophication and river-engineering are likely to represent more important threats to the river macrophyte vegetation of Central Europe than climate warming. Evidence in support of this conclusion is the observed increase in R-strategists and the decrease in mean SLA in our data, and the finding of Garniel (1999) that, after decades of intensive water course maintenance with machines, the vegetation in many running waters of Schleswig Holstein (northern Germany) mainly consists of mowing-tolerant species like *Sparganium emersum*, *Nuphar lutea* and *Potamogeton pectinatus*, which place their roots several decimetres deep in the sediment.

Conclusions

Our resampling study documents the long-term change in the running water macrophyte vegetation of four regions that may be representative for large parts of the northern German diluvial lowlands. Both the decrease in the regional species pool and in plot-level diversity were dramatic with the consequence that most water courses are colonized nowadays by only species-poor, relatively uniform communities that contain a high proportion of species adapted to disturbance. While currently red-listed macrophytes were still relatively widespread in the 1950s, they are in many cases highly endangered in our times. This is, for example, the case for *Myriophyllum alterniflorum*, *Isolepis fluitans* (both endangered), *Zannichellia palustris* (near-threatened) and some magnopotamid species that have vanished in more than 50 % of the sites visited, where they still occurred in the 1950s. The likely causes of the impoverishment are continued nutrient input from intensively managed agricultural land that caused the disappearance of oligo- and mesotraphent species and the restructuring of most river beds together with the continuous maintenance of water courses; these measures resulted in the loss of more stagnant stream and river habitats where stress-intolerant species are able to persist. Thus, measures to reduce the nutrient load in rivers and to re-naturalize the flow regime in selected river sections are urgently needed in order to halt and reverse the catastrophic loss of phytodiversity in Central European lowland rivers. Both, biodiversity conservation and flood risk management, would profit from the creation of floodplain retention areas with a variety of stagnant freshwater habitats. The loss of most specialist species in the macrophyte flora largely devaluates this group in its role as an indicator of environmental quality in streams and rivers.

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Chapter 4

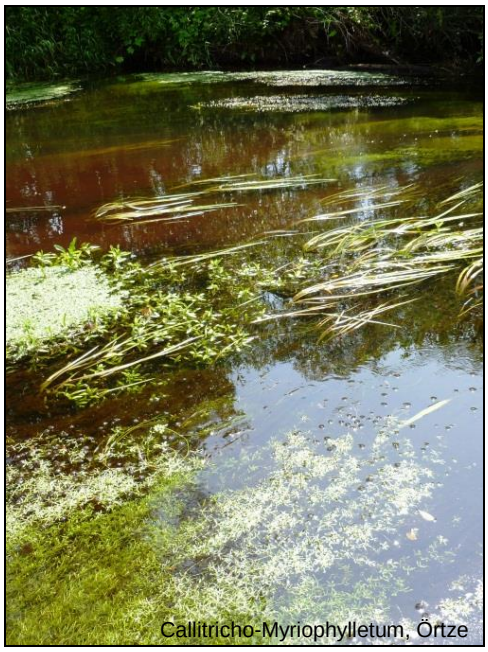
Sixty years of change in the macrophyte vegetation of north-west German running waters: a community- and landscape-level analysis

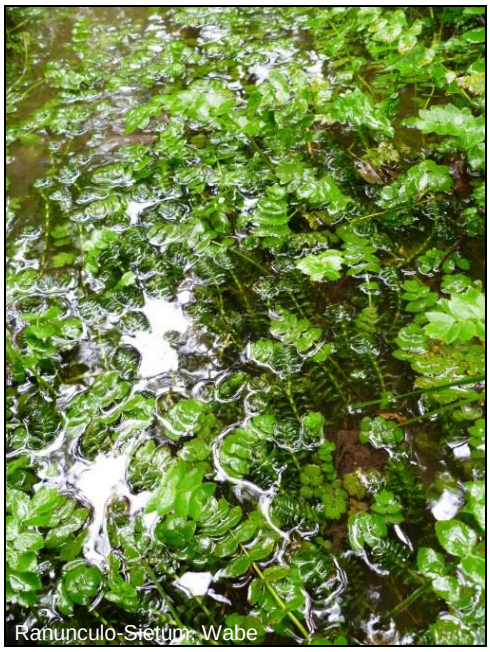
Kristina Steffen & Christoph Leuschner

(submitted)


Ranunculetum fluitantis, Emmer


Sparganio-Elodeetum, Aller


Callitricho-Myriophylletum, Örtze


Ranunculo-Sietum, Wabe

Abstract

Long-term change in the macrophyte assemblages of 70 streams and rivers in four regions of north-west Germany was examined with a semi-permanent plot design based on 337 historical vegetation relevés from the 1950s that were repeated in 2010/2011. Plant assemblages were classified with two alternative phytosociological approaches based on character species and/or dominant species. Over the ~60 years, the structure and composition of the vegetation changed profoundly in all four regions, even though local differences in vegetation dynamics existed. In general, stands assignable to the alliances Ranunculion (Batrachion) and Potamogetonion (assemblages dominated by submerged rooted plants) decreased greatly in frequency while Nymphaeion stands (dominated by floating-leaved rooted plants) increased. Communities weakly characterized by diagnostic species increased revealing losses of specialist taxa and homogenization of the assemblages; macrophyte community diversity at the landscape level decreased. Eutrophication, hydraulic engineering and regular maintenance works in the water courses are discussed as likely causes of the vegetation change. We conclude that decade-long human impact on river hydraulics and chemistry has significantly reduced both plot-level species richness and community diversity at the landscape level, profoundly altering the relative abundance of the assemblages.

Keywords: Ellenberg indicator values, eutrophication, phytosociological classification, reduction in community diversity, re-sampling study

Introduction

Streams and rivers and their macrophyte vegetation are among the ecosystems most severely affected by agricultural intensification in the world's industrialized regions (Malmqvist & Rundle 2002, Ellenberg & Leuschner 2010). In the lowlands of northern Central Europe, for example, the amounts of N and P fertilizers applied to arable fields and grasslands increased more than fourfold from the 1950s to the 1980s resulting in greatly increased nutrient inputs into the running waters and causing widespread eutrophication (Gelbrecht et al. 1996, Behrendt et al. 1999). In the course of floodplain melioration, many river beds were straightened and deepened to improve landscape drainage, and adjacent semi-aquatic habitats transformed to agricultural land. During the last four to six decades, the combined impact of nutrient addition and river engineering has fundamentally altered the structure of the macrophyte vegetation in the water courses of many Central European regions (Herr et al. 1989a, Fischer 1995, Whitton et al. 1998, Schütz et al. 2008). While long-term monitoring data of macrophyte vegetation change are very scarce, a number of re-

sampling studies in Central, Western or Northern Europe documented reductions in plot-level diversity and impoverishment of the regional macrophyte species pool (e.g. Riis & Sand-Jensen 2001, Bouxin 2011, Steffen et al. 2013). For certain target species or genera with indicative value (such as *Potamogeton*), more detailed information does exist (Wiegleb et al. 1991, Preston 1995). However, the bulk of studies focused on relatively small areas with the consequence that a broader perspective of long-term change and impoverishment in the macrophyte vegetation has not yet emerged. The existing data demonstrate that change has not only reduced plot-level diversity in many macrophyte communities, but has also resulted in marked shifts in the species composition of the assemblages and in the relative abundance of the communities at the landscape scale. There is a need for cross-regional assessments of long-term community change in the macrophyte vegetation of running waters in Europe and elsewhere. This information could help to improve conservation programs for the endangered stream and river biota and it would allow conclusions on long-term habitat quality change in running waters beyond the insights gained from official monitoring programs that cover only a few hydro-chemical and -biological state parameters.

The community-based assessment of macrophyte vegetation change is hampered by the fact that vegetation classification in limnic habitats is more difficult than in most terrestrial habitats (Pearsall 1918, Haury & Muller 2008). Problems identified include the considerable morphological plasticity of many species (Weber 1976), an often heterogeneous vegetation data basis with non-consistent plot sizes (Wiegleb 1981), the relatively low number of obligate hydrophytes in many communities, and the fact that many macrophyte species can form monospecific stands covering several square metres (Sculthorpe 1967, Best 1988). Consequently, a number of concepts of macrophyte community classification have been proposed, but consensus on the most suitable method does not exist. The approaches either adopt the traditional phytosociological association concept based on the identification of characteristic species (e.g. Roll 1939, Weber-Oldecop 1970, Preising et al. 1990, Pott 1995), use morphological growth forms for classification (Herr et al. 1989b, Dawson et al. 1999), apply numerical methods and similarity or dissimilarity indices for vegetation clustering (Paal et al. 2007), or combine two or more of these concepts (Berg et al. 2004, Chytrý 2011). There has been some discussion on the usefulness of applying phytosociological approaches to aquatic plant assemblages. In studies carried out in the tradition of the Zürich-Montpellier school, the criterion of homogeneity often has led to the selection of relatively small relevé sizes (Braun-Blanquet 1964, Passarge 1982) resulting in nearly as many aquatic plant associations described as there are hydrophytic macrophyte species (Rennwald 2000). Since about the 1970s, the sampling of larger plots became more common and stretches of 50 m to several kilometres length along rivers of any size were investigated (e.g. Holmes & Whitton 1977, Kohler 1978, Riis et al. 2000, van de Weyer 2001). Such large

plots seem to be quite suitable for classification, because they are more likely to contain characteristic combinations of taxa and not only species-poor mono-dominant stands, but plots of large size will inevitably cover habitat mosaics due to gradients in water depth, current velocity, shading intensity and other factors, thus violating a basic assumption of the community concept.

In this study, which is complementary to an earlier study analysing species diversity changes in north-west German running waters (Steffen et al. 2013), we attempt to analyse the long-term change in the macrophyte assemblages of streams and rivers in north-west Germany over six decades with a focus on the community and landscape level. We conducted a re-sampling study in more than 300 semi-permanent vegetation plots in four regions covering a broad variety of stream and river habitats. The regions may be representative for large parts of the diluvial lowlands of northern Central Europe. By comparing the species composition and relative abundance of macrophyte assemblages in the regions for the 1950s and for 2010/2011, we addressed the following questions: (1) How has macrophyte community structure and the vegetation mosaic in streams and rivers changed as a consequence of agricultural intensification and water course management since the 1950s? (2) What do the individual developments of the macrophyte assemblages in the four studied regions tell us about the drivers of change? And (3) does a community and landscape level analysis increase our understanding of anthropogenic vegetation change beyond insights already gained from comparative plot-level diversity analyses?

Materials and methods

Study area

The 70 sampled streams and rivers are located in four regions of the north-west German Pleistocene lowlands (federal states of Lower Saxony, Schleswig-Holstein and North Rhine-Westphalia): (1) the Ems-Hunte moraine country with acid, base-poor moraine soils and bogs and (2) the Lüneburg Heath (including the Aller lowlands) with base-poor, sandy soils, both formed by the penultimate (Saale) Ice Age, (3) the northern Harz foothills (including some sites at the base of the Weser-Leine uplands) with fertile Pleistocene loess, and (4) the eastern Holstein moraine country with more base-rich young moraine soils of the last (Weichsel) Ice Age (Figure 4.1). The studied streams and rivers cover a broad range of water course types with small to medium size (1–40 m in diameter and 0.2–2 m in depth), current velocities between 0 and 50 cm s^{-1} and sandy to loamy sediments partly overlain by organic deposits or gravel. The catchments of all rivers are part of the cultural landscape of north-west Germany consisting of a mosaic of arable fields, pastures, meadows, forests and settlements. While the river sediments of the study regions 1 and 2 are base-poor and those of the regions 3 and 4 moderately base-rich, all rivers are receiving considerable nutrient

loads from the adjacent intensively managed agricultural land in recent time. Due to the oceanic influence, the north-west German lowlands have a humid climate, characterized by relatively warm summers and relatively mild winters with short frost periods. Mean annual temperatures range around 9 °C, with the lowest mean temperature in January (0.4 °C Braunschweig, Lower Saxony) and the highest mean temperature in July (17.2 °C Hannover, Lower Saxony). The average annual precipitation ranges between 656 mm yr^{-1} (Hannover) and 754 mm yr^{-1} (Kiel, Schleswig-Holstein) (climate data taken from Deutscher Wetterdienst 2013).

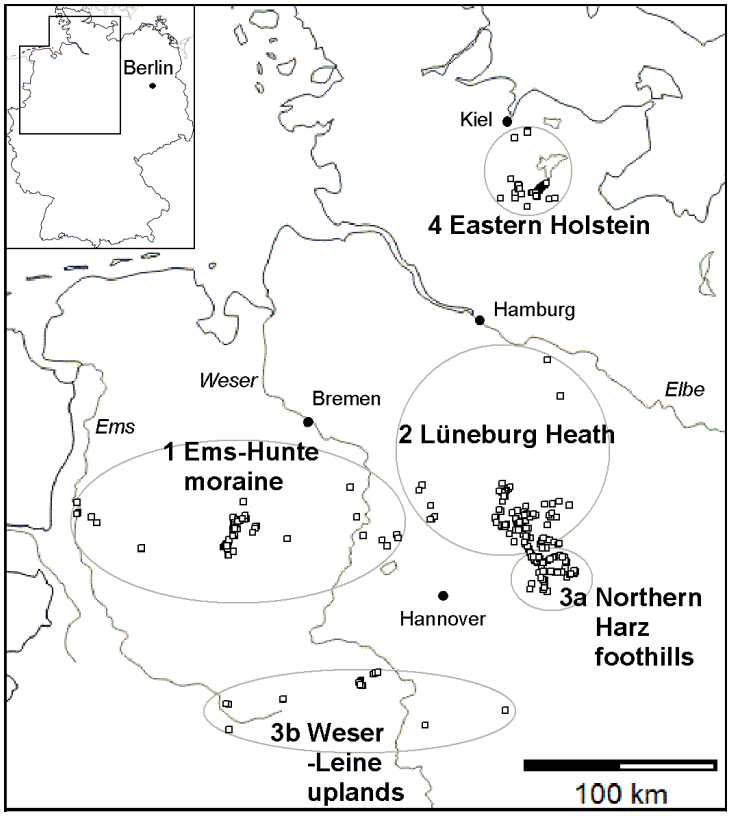


Figure 4.1 Location of the study sites (open squares) within four regions of NW Germany: region 1 = Ems-Hunte moraine, region 2 = Lüneburg Heath (including the Aller lowlands), region 3 = (a) northern Harz foothills and (b) base of the Weser-Leine uplands and region 4 = eastern Holstein moraine

Historical data

We used 337 historical vegetation relevés taken from the Reinhold-Tüxen-Archiv, Hannover (Hoppe 2005; sampled by R. Alpers, R. Tüxen and A. von Hübschmann) and from the literature (Roll 1939, Weber-Oldecop 1969), dating back to between 1936 and 1969, which are referred to as 1950s data. Plot sizes ranged between 1 and 100 m². Since it has to be assumed that species identification in the genera *Callitriche* and *Ranunculus* was not always appropriate in former times, the taxa *Callitriche cophocarpa*, *C. obtusangula*, *C.*

palustris, *C. platycarpa* and *C.* x *vigens* were summarized as *C. palustris* agg., while *Ranunculus aquatilis* and *R. peltatus* were summarized as *R. aquatilis* agg. The aggregates were used throughout the entire analysis and are referred to as species. As mentioned by Berg et al. (2004), it cannot necessarily be taken for granted that, in historical relevés, Lemnetea species were always noted during the documentation of a Potamogetonetea assemblage. However, in the case of the historical data used by us, lemnid species are frequently present in the Potamogetonetea relevés of all authors with the exception of the data of von Hübschmann (5 relevés of this author were included) suggesting that Lemnetea species were in most cases not ignored.

Sampling design and field methods

The historical vegetation relevés were repeated in the summers of 2010 and 2011 at the original sampling locations as indicated in the description or at the closest point, where vegetation was well developed. We sampled a plot size of 100 m². Vegetation was inspected by means of wade trousers and a telescopic rake. Within a plot, the cover values of all plants rooting below the water surface were recorded. Additionally, the width and depth of the reach as well as the current velocity in the stream line (drift method, Weber-Oldecop 1969) were determined.

Data analysis

Seventy-nine species (all hydrophytes and those helophytes that are mentioned as character species in the literature) were included in the analyses. To relevés taken with the Braun-Blanquet cover class scores, we assigned the central numerical value of that class. We applied two alternative classification systems to the data set. First, the relevé material was classified by means of phytosociological character species following Preising et al. (1990), whose system was developed specifically for the freshwater plant assemblages of the north-west German lowlands, and after Schubert (2008) for bryophyte-dominated communities. In this approach, helophytes were only considered for classification in relevés that contained no hydrophytes. Since lemnid species are displaceable in running waters, relevés were only grouped as Lemnetea communities, if no rhizophytic hydrophytes were present.

Alternatively, the relevés were classified with the recently introduced phytosociological approach of Chytrý (2011) developed for the macrophyte vegetation of the Czech Republic. As a modification from this approach, we used lower cover threshold values for the assignment of relevés to an association: For reducing the proportion of relevés that were not assignable to defined associations, we adopted in the historical data set thresholds of 15% and 25%, respectively, where 25% and 50% had been defined in the Czech system.

In the 2010/2011 data, we set the cover threshold even to 2 %, because the recent plot size was on average larger than in the 1950s and we sought for a conservative assessment of community-level change by defining a low cut-off level which again reduced the number of non-assignable macrophyte stands. In the approach of Chytrý (2011), character species of the Batrachion associations are given a higher indicative value than those of the Potamogetonion associations, followed by those of Nymphaeion associations and finally by character species of the Lemnetea and Phragmito-Magno-Caricetea communities. The 56 historical and 128 recent relevés, that were not assignable after applying these rules, were grouped with the association to which the most similar relevé according to the Bray Curtis similarity index had been classified. The Bray Curtis index is defined as:

S_{BC}= 2W/(A+B),

where W is the sum of the lower cover values from each pair of shared species of the samples A and B, A is the sum of the cover values of all species in sample A, and B is the sum of the cover values of all species in sample B.

Unweighted Ellenberg indicator values (EIVs) for temperature, soil reaction (pH) and nutrients (Ellenberg et al. 2001) were calculated as means per plot and used as an indicator for environmental conditions. Differences between several groups of relevés were tested for significance ($p<0.05$) with a Tukey post hoc test. A detrended correspondence analysis (DCA, Hill & Gauch 1980) was conducted with the software Canoco 4.56 (Biometrics, Wageningen, NL). For every pair of historical and recent relevés at a given site, successional vectors translated to the origin (McCune et al. 2002) were calculated with the program PCOrd 5.1 (MjM Software, Gleneden Beach, US). The same was done for the summarized data for each of the 70 investigated running waters. The vector lengths were determined with the Pythagorean Theorem to analyze the vegetation change over time at the regional level and in relation to environmental and hydrographic factors. The factors were correlated with the DCA axes in a post hoc manner. Spearman rank correlation was used, since the axes scores and successional vector lengths were not normally distributed; the significance levels for the correlations are not based on a permutation test, but are given to indicate the strengths of the relationships. For placing the communities in a two-dimensional niche space defined by current velocity and the EIV for nutrients, the minima and maxima of the two variables observed in the respective vegetation unit were used. The average similarity (S_{BC}) between the historical and recent assemblages was calculated from all possible pairs of data summarized per river (species lists and numbers of occurrences) and compared with a Wilcoxon test. All statistical tests were carried out with the software SPSS 15 (SPSS Inc., Chicago, USA).

Results

Vegetation change in river macrophyte assemblages over 60 years as revealed by the classification after Preising et al. (1990)

In total, 79 taxa of higher plants and mosses (60 hydro- or amphiphytic and 19 helophytic taxa) were recorded in the streams and rivers of the four study regions (Tables 4.1a and 4.1b in the Appendix). Applying the phytosociological classification system of Preising et al. (1990), ninety-five percent of the relevés taken in historical time or in 2010/2011 could be assigned to phytosociological units within the class Potamogetonetea, which contains all submerged or floating-leaved, rooted vascular plant vegetation types of European fresh waters (Table 4.2). About five percent of the relevés in 2010/2011 (none in the 1950s) referred to the class Lemnetea, i.e. free-floating macrophyte carpets at the surface without presence of rhizophytic hydrophytes. Within the principal macrophyte class Potamogetonetea, all three orders recognized by Preising et al. (1990) were represented by relevés. The most widespread assemblage at the association level was in the 1950s the Callitricho-Myriophylletum (in the alliance Ranunculion fluitantis and the order Callitricho-Batrachietalia) with ~28 % of all relevés, followed by the Potamogetonetum lucentis (in the alliance Potamogetonion lucentis and the order Potamogetonetalia; 12 %). In historical time, 18 % of the relevés referred to assemblages characterized by pondweeds (order Potamogetonetalia) and 15 % to relevés characterized by floating-leaved, rooted Nymphaeetalia assemblages. About six decades later, the relative frequency of the most widespread association, the Callitricho-Myriophylletum, has greatly decreased (-32 %). Large decreases were also recorded for most of the pondweed assemblages, notably the formerly widespread Potamogetonetum lucentis (-78 %) and the assemblages in the order Potamogetonetalia in general (-58 %). The number of relevés assigned to the Potamogetonetum lucentis remained constant over time in the Lüneburg Heath (region 2), but decreased greatly in the Ems-Hunte and eastern Holstein regions, where this community formerly occurred at 22 and 14 sites, respectively, and decreased to three sites each in 2010. Marked decreases were also found in the once more frequent Ranunculion fluitantis assemblage Ranunculo-Sietum (-47 %).

In contrast, more frequently occurring in 2010/2011 were assemblages of the Nymphaeetalia order (+44 %) with the association Sparganio-Elodeetum (+46 %). The Myriophyllo-Nupharetum and the Sparganio-Elodeetum stands occur only in streams with low current velocities (Figure 4.2a) and were mainly restricted to region 1 (Ems-Hunte moraine) in both surveys. Water lens carpets (class Lemnetea) apparently occurred more frequently in running waters in 2010/2011 than in the 1950s, with fragments of the alliances Lemnion gibbae and Lemnion trisulcae found in region 4 (eastern Holstein), where rivers often flow through lakes with stagnant waters. Two moss-dominated relevés originating from

region 3 (northern Harz foothills) from 2010/2011 were assigned to the class Fontinalietea, a few helophytic assemblages to the class Phragmitetea (reed vegetation). Among the each 337 relevés taken in the two surveys, the number of relevés assignable to the association level decreased by a fourth from 198 (59 % of the total) in the 1950s to only 145 (43 %) in 2010/2011, indicating that more than half of the recent relevés lacked diagnostic taxa for the association level.

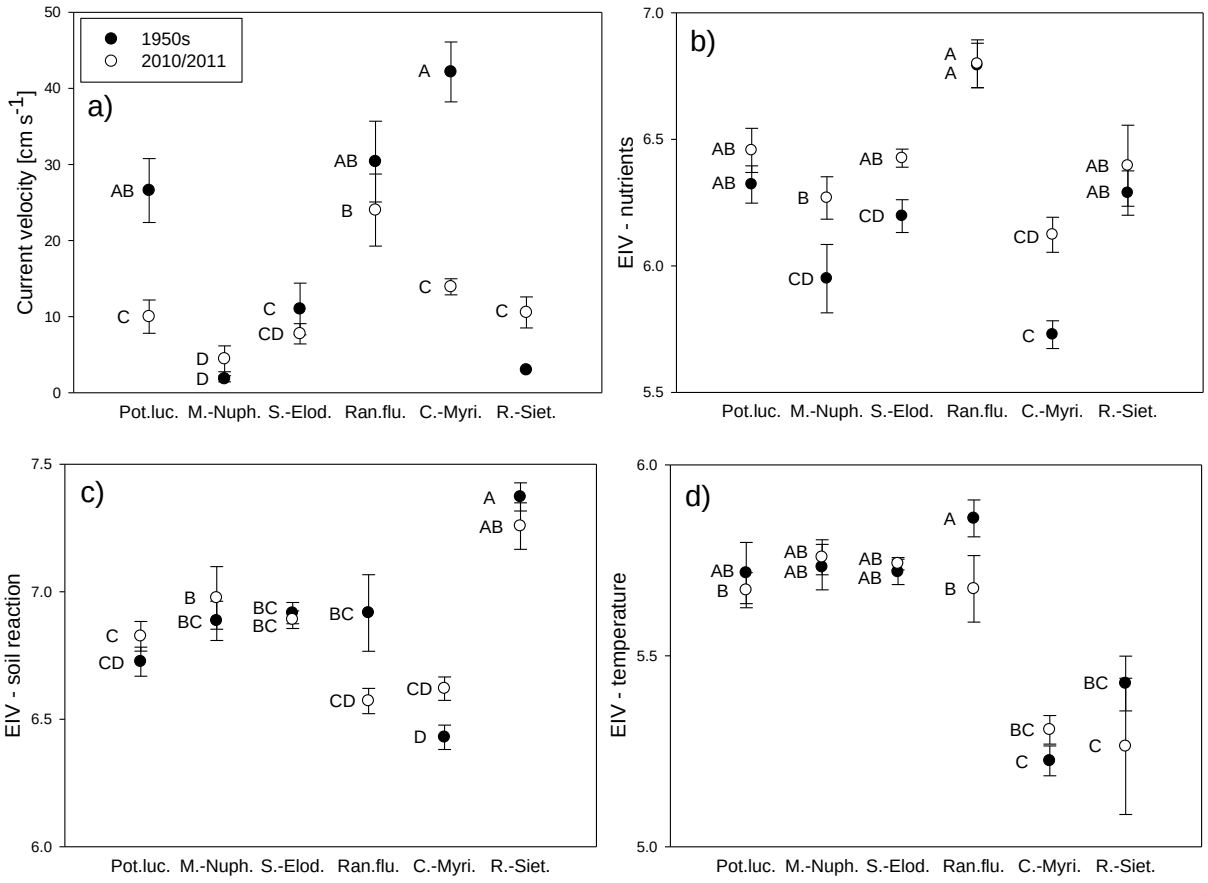


Figure 4.2 (a) Current velocity and mean Ellenberg indicator values for (b) nutrients, (c) soil reaction and (d) temperature in six important macrophyte associations in the 1950s and 2010/2011 (198 relevés from the 1950s and 145 relevés from 2010/2011; given are means ± SE). Different letters indicate significant differences between the periods. Pot.luc. = Potamogetonetum lucentis, M.-Nuph. = Myriophyllo-Nupharetum. S.-Elod. = Sparganio-Elodeetum, Ran.flu. = Ranunculetum fluitantis, C.-Myri. = Callitricho-Myriophylletum, R.-Siet. = Ranunculo-Sietum. Only one Ranunculo-Sietum relevé from the 1950s contained information about current velocity

Table 4.2 Number of relevés assignable in the 1950s or in 2010/2011 to macrophyte classes, orders, alliances or associations according to the phytosociological system after Preising et al. (1990). At the order, alliance and association level, only syntaxa of the most widespread class Potamogetonetea are listed. In the two survey periods, 337 and 327 relevés were analyzed. The change between the 1950s and 2010/2011 is expressed in percent loss or gain in frequency

	No. of relevés in the 1950s	No. of relevés in 2010/2011	Change [%]
Lemnetea	-	18	
Potamogetonetea	336	305	-9.2
Phragmitetea	1	7	+85.7
Platyhypnidio-Fontinalietea antipyreticae	-	2	
No macrophyte vegetation present	-	5	
Orders in Potamogetonetea			
Potamogetonetalia	59	25	-57.6
Nymphaeetalia	52	92	+43.5
Callitricho-Batrachietalia	219	183	-16.4
Alliances in Potamogetonetea			
Potamogetonion graminei	1	-	
Potamogetonion lucentis	41	11	-73.2
Potamogetonion pusilli	16	10	-37.5
Nymphaeion albae	40	75	+46.7
Hydrocharition	2	-	
Ranunculion fluitantis	212	171	-19.3
Associations in Potamogetonetea			
Potamogetonetum lucentis	40	9	-77.5
Myriophyllo-Nupharetum luteae	12	11	-8.3
Sparganio-Elodeetum	24	44	+45.5
Ranunculetum fluitantis	10	7	-30.0
Callitricho-Myriophylletum alterniflori	95	65	-31.6
Ranunculo-Sietum erecti-submersi	17	9	-47.1
Assignable to association level	198	145	-26.8
Assignable only to alliance level	115	135	+14.8
Assignable only to order level	18	47	+61.7
Assignable only to class level	6	5	-16.7

Vegetation change as revealed by the classification system after Chytrý (2011)

When applying the classification system of Chytrý (2011), nearly all 674 relevés could be assigned to one of 30 associations of this system (including the *Elodea nuttallii* dominance stand). Assignment was not possible for five relevés that referred to river sections devoid of macrophyte vegetation in 2010/2011. The Czech system does not contain the level of orders, but a rough congruence between Preising's Batrachietalia, Potamogetonetalia and Nymphaeetalia orders with Chytrý's Batrachion, Potamogetonion and Nymphaeion alliances does exist. Analysis of community change based on the Chytrý (2011) classification indicated that only a few historical Batrachion and Nymphaeion stands were replaced by Potamogetonion stands in 2010/2011, while many of the former Potamogetonion stands

changed into Lemnetea and Nymphaeion stands in recent time (Table 4.3). The proportional increase of macrophyte communities assignable to the class Lemnetea and the alliance Nymphaeion, being typical for potamal water courses, as found in the Preising approach was confirmed with the Chytrý approach (Figure 4.3). Especially in the regions 1 (Ems-Hunte) and 4 (Holstein), communities adapted to very low current velocities increased in the rivers and streams. Dominance stands of *Elodea nuttallii* were exclusively observed in the regions 1 and 2.

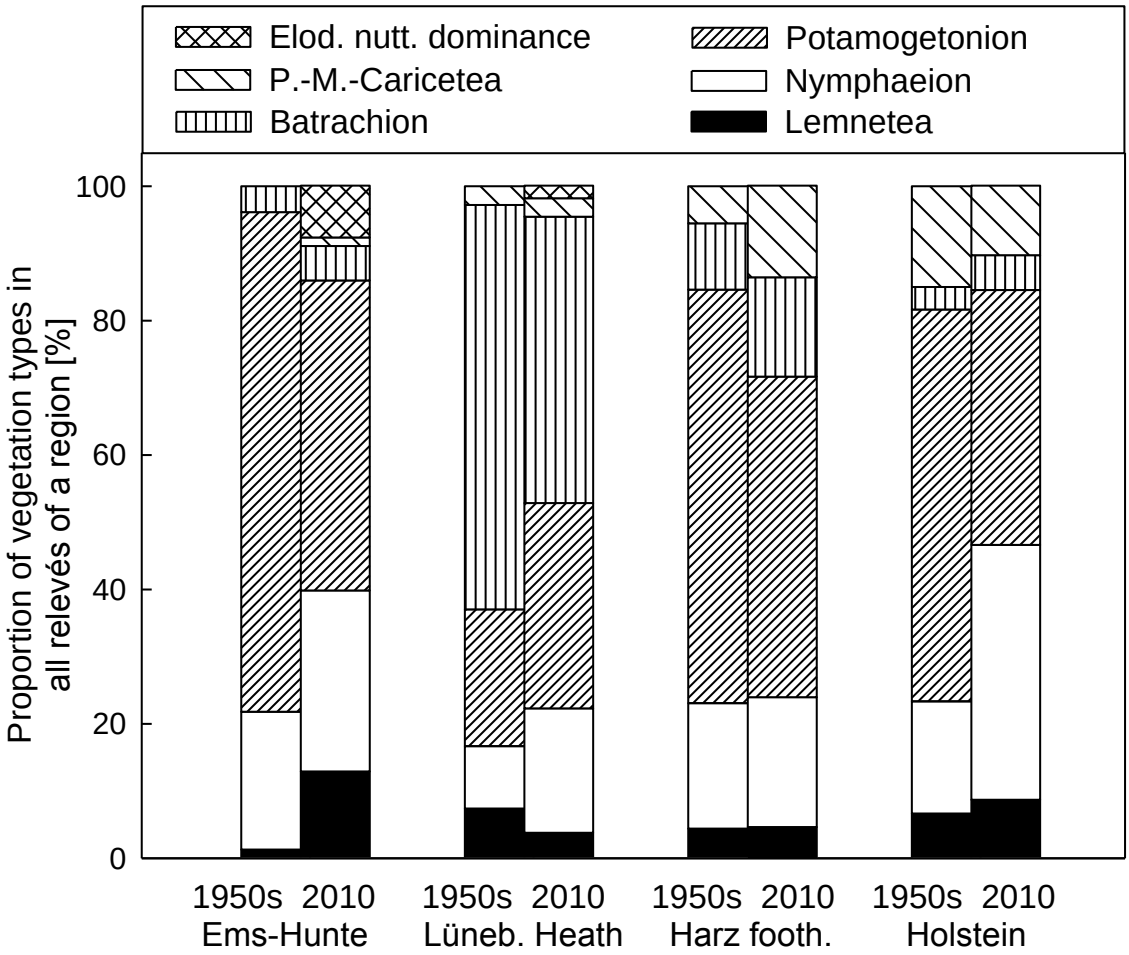


Figure 4.3 Proportion of different synsystematic groups of macrophyte assemblages (classification after Chytrý 2011) in the total number of relevés of the four studied regions in the 1950s and 2010/2011 (78 semi-permanent plots in region 1, 108 in region 2, 91 in region 3 and 60 in region 4)

Table 4.3 Temporal change in the macrophyte vegetation stands as mirrored in the system of Chytrý (2011) with the assignment of the relevés to associations in the 1950s (rows) and in 2010/2011 (columns) (associations 1 to 31 with 1= Lemnetum minoris, 2= Lemnetum gibbae, 3= Lemno-Spirodeletum polyrhizae, 4= Lemnetum trisulcae, 5= Lemno-Utricularietum, 6= Ceratophylletum demersi, 7= Hydrocharitetum morsus ranae, 8= Potamogetonetum crispi, 9= Potamogetonetum natantis, 10= Potamogetonetum pectinati, 11= Potamogetonetum pusilli, 12= Elodeetum canadensis, 13= Potamo pectinati-Myriophylletum spicati, 14= Groenlandietum densae, 15= Potamogetonetum tenuifolii, 16= Potamogetonetum zizii, 17= Potamogetonetum friesii, 18= Potamogetonetum lucentis, 19= Potamogetonetum denso-nodosi, 20= Potamogetonetum crispo-obtusifolii, 21= Potamogetonetum perfoliati, 22= Scirpo fluitantis-Potamogetonetum polygonifolii, 23= Parvo-Potamo-Zannichellietum pedicellatae, 24= Nymphaeo albae-Nupharetum luteae, 25= Nymphaeetum albae, 26= Ranunculetum fluitantis, 27= Callitricho hamulatae-Ranunculetum fluitantis, 28= Myriophylletum alterniflori, 29= Glycerio-Sparganietum, 30= Beruletum erectae, 31= *Elodea nuttallii* dominance stands and no. veg.= vegetation-free). The numbers give the number of assigned stands (relevés). Numbers in grey fields refer to vegetation stands assigned to the same association in the 1950s and in 2010/2011

	Lemnetea					Potamogetonion												Nym-phaeion	Batra-chion		P.-M.-Caricetea					
Asso-ciation	1	3	4	5	6	8	9	10	11	12	13	18	19	20	21	23	24	26	27	28	29	30	31	no veg.	∑
1							1					1				1	2	1	3			1			10
2											1						1								2
3							1																		1
4																					1				1
5				1																					1
7																	1	1							2
8				1	1	1		1			2	1					2		1						10
9							6	4	2	5	3				1		7		1						29
10	1						2	9			1				3		4	1					1		22
11						1	1				3					1	3								9
12	2					1				2					3		7			2	2		1	1	21
13							2	1			1						1								5
14																	1					1			2
15														1					1						2
16																	1								1
17	1										2													1	4
18	3			1		2				3	1	4	3		2		9						1	1	30
19															1						1				2
20															1										1
21		1					1	2		2		2			1		5	1	1				1		17
22																	1								1
23	1					1										2	2			2		7			15
24	1	2	1		3	1	2	2	1	1	5	3				1	20	1	2		1	1	2	2	52
25																	1								1
26						1		1	1							1	2	5				1			12
27	1	2					2	1		3	2	1				2	4	5	9	14	2		2		50
28							1			2	1						2		2	8	1				17
29																				1					1
30						1		1							3		4	1		3	2	1			16
∑	10	5	1	3	4	9	19	22	4	18	22	12	3	1	15	8	80	16	20	30	10	12	8	5	337

Environmental change at the community level since the 1950s

The detrended correspondence analysis of all relevés assignable to the association level in Preising's system showed a relatively clear division between the communities of potamal, more gently flowing water course reaches, which represent units of the Nymphaeion albae and Potamogetonion lucentis alliances, and those of smaller water course reaches with higher current velocities, which were assigned to the Ranunculion fluitantis alliance (Figure 4.4). While the first DCA axis revealed a strong negative correlation with various abiotic site factors, notably water depth and the EIVs for temperature, soil reaction and nutrients, and a positive relation to current velocity, the second axis correlated positively with time (sampling years) and negatively with current velocity (Table 4.4). Analysis of environmental change over time in waters colonized by the six most frequent macrophyte associations showed that in two of the six communities (Myriophyllo-Nupharetum and Sparganio-Elodeetum), the mean EIV for nutrients was significantly higher in 2010/2011 than in the 1950s (non-significant trend also in the Callitricho-Myriophylletum). In the Ranunculetum fluitantis, the mean EIV for nutrients was high in both periods (c. 6.7; Figure 4.2b). No significant change over time was found for the mean EIV for soil reaction; the Ranunculo-Sietum (only recorded in region 3: Harz foothills) had a particularly high mean EIV for soil reaction in both periods (Figure 4.2c). Interestingly, we found in none of the six assemblages a significant increase in the EIV for temperature over the six decades (Figure 4.2d), even though the communities differ considerably in their apparent thermal requirements. The Ranunculetum fluitantis showed even a significant decrease in EIV-T between the 1950s and 2010/2011. The current velocity measurements indicate a broad range of characteristic flow ranges for the six assemblages with nearly stagnant waters characterizing the sites of the Myriophyllo-Nupharetum and highest velocities found at the sites of the Ranunculetum fluitantis and Callitricho-Myriophylletum (Figure 4.2a). At the sites of the Potamogetonetum lucentis and Callitricho-Myriophylletum, current velocity has apparently decreased since the 1950s. Linking the pairs of plots of a given site with successional vectors in the ordination space revealed an overall change among the communities in the negative direction of DCA axis 1. This axis correlated negatively with river width (reach size) and the EIVs for nutrients and temperature (Figure 4.5, Table 4.5 in the Appendix), thus pointing to general increases in nutrient availability, temperature and river width over the 60 years. When grouped by region, the successional vectors of the region 2 (Lüneburg Heath) correlated positively with increasing EIVs for temperature, soil reaction and nutrients and that of region 4 (eastern Holstein) with river width and depth (Table 4.6). Summarizing the vegetation change observed in each of the 70 rivers confirmed a general path of vegetation succession over the 60 years, which followed rising nutrient availabilities and an increase in water course size reflecting river engineering works (Figure 4.6, Table 4.7

in the Appendix and Table 4.8). The average similarity between the macrophyte assemblages of all possible pairs of rivers was significantly ($p<0.001$) lower in the historical (S_{BC}=0.22) than in the recent (0.25) vegetation data. Figure 4.7 suggests that the historical macrophyte assemblages seem to have occurred under a wider range of nutrient availabilities and current velocities than the recent assemblages.

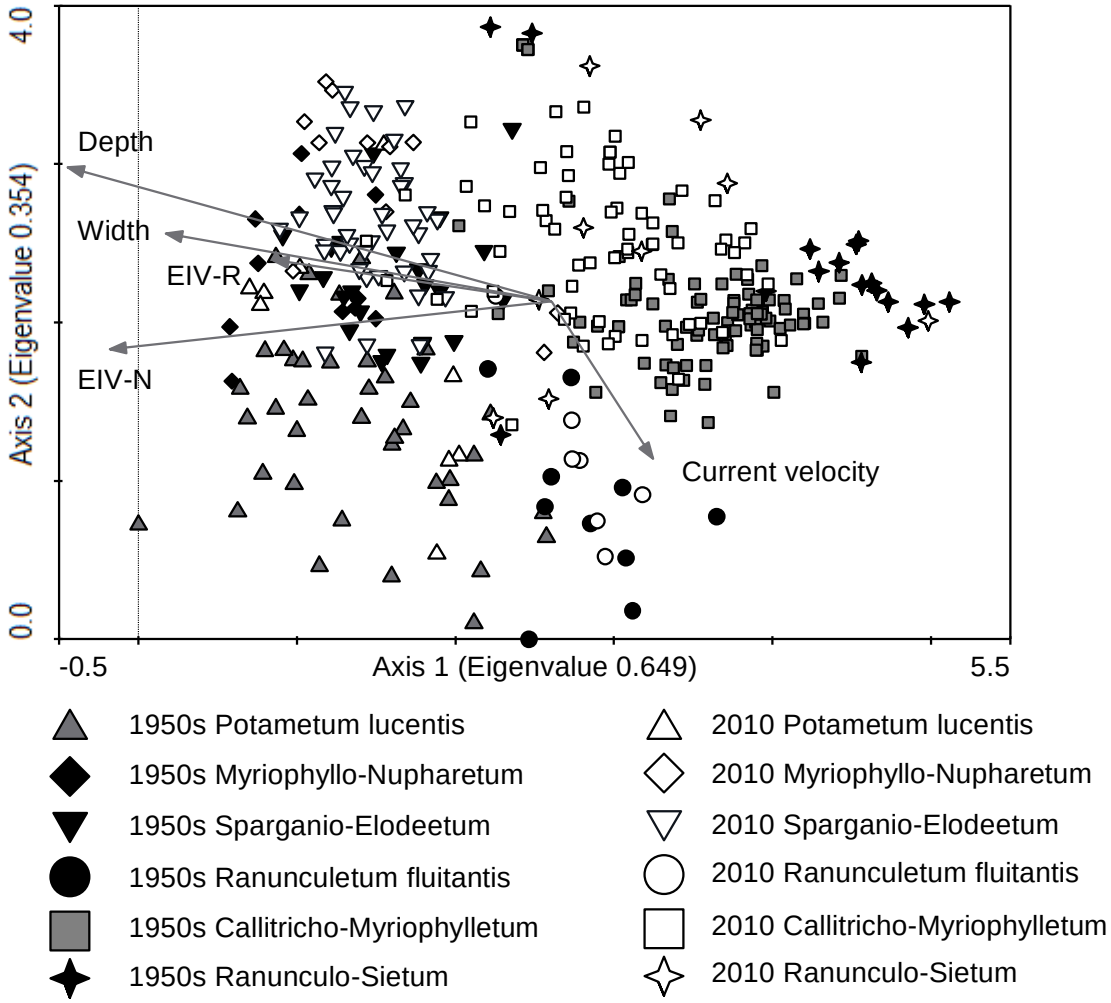


Figure 4.4 DCA graph showing all relevés that could be assigned to associations after Preising et al. (1990) (198 relevés from the 1950s and 145 relevés from 2010/2011). Environmental variables were included as additional information. See Table 4.4 for correlations of the DCA axes with environmental factors

Table 4.4 Correlation coefficients after Spearman and p values of the relationships between time (sampling years) or environmental variables and DCA axes 1 and 2 for 343 relevés that were classified to the association level following Preising et al. (1990)

Parameter	r DCA axis 1	p	r DCA axis 2	p
Time	-0.20	***<0.001	0.44	***<0.001
Current velocity	0.53	***<0.001	-0.35	***<0.001
Reach width	-0.32	***<0.001	-0.01	0.854
Reach depth	-0.49	***<0.001	0.02	0.709
EIV - temperature	-0.59	***<0.001	-0.09	0.099
EIV - soil reaction	-0.22	***<0.001	0.14	*0.012
EIV - nutrients	-0.34	***<0.001	0.08	0.138

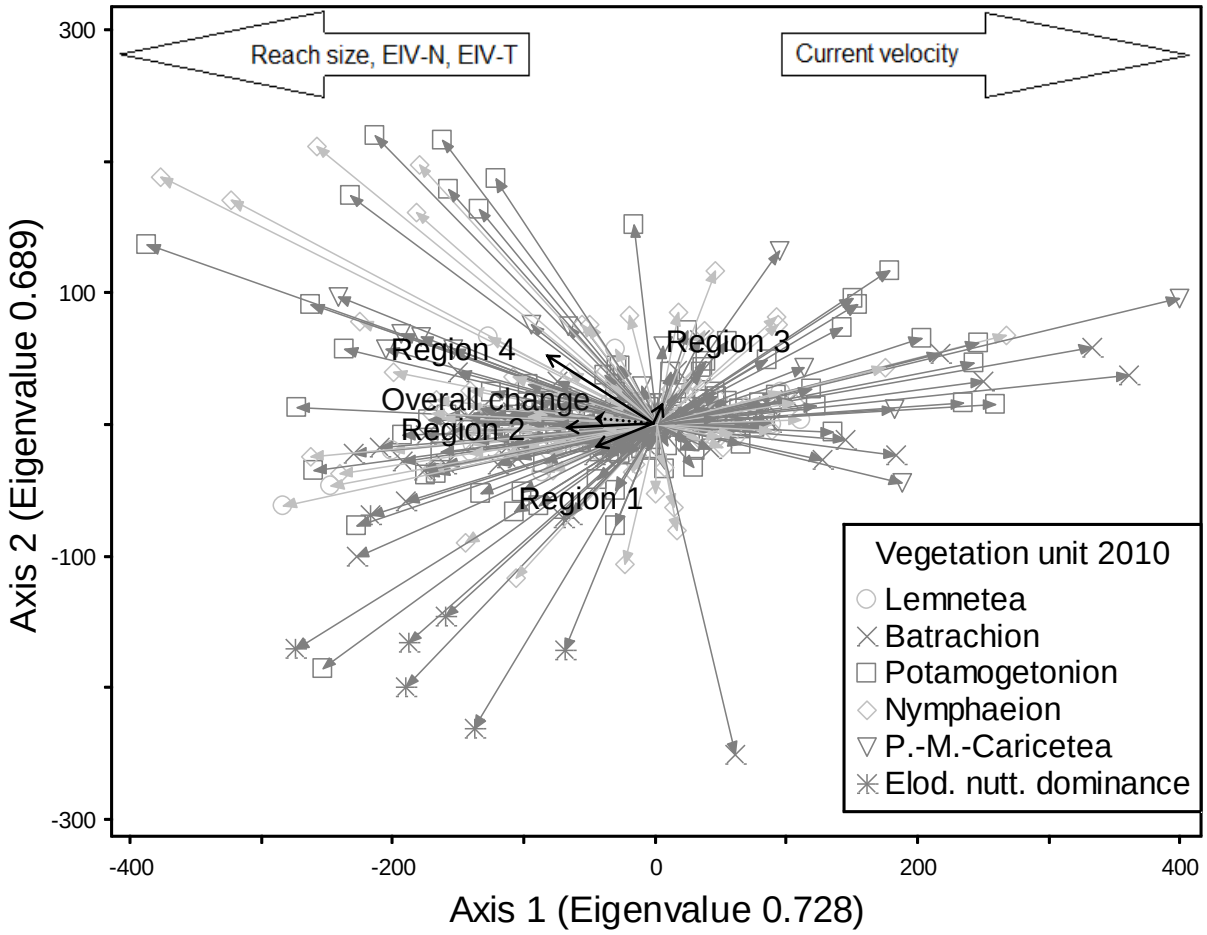


Figure 4.5 Successional vectors translated to origin (1950s) of 325 pairs of vegetation relevés (1950s – 2010/2011 contrast) assigned to a vegetation unit according to the system of Chytrý (2011) or referring to *Elodea nuttallii* dominance stands with the arrow pointing to the corresponding 2010/2011 relevé (grey arrows). The resulting direction of overall change is indicated with a dotted arrow, the directions of change for the relevés of each region are indicated with black arrows. Seven relevé pairs containing outliers were omitted. See Table 4.5 in the Appendix and Table 4.6 for correlations of the DCA axes and the successional vectors with environmental variables

Table 4.6 Correlation coefficients after Spearman and p values of the relationships between environmental variables (changes over time per plot) and the successional vector lengths for a total of 650 relevés that were used for the trajectory analysis, differentiated after regions

Parameter	All regions	p	Region 1	p	Region 2	p	Region 3	p	Region 4	p
Change in current velocity	-0.11	0.053	0.03	0.827	0.08	0.427	-0.09	0.393	0.08	0.563
Change in reach width	0.04	0.525	0.19	0.102	0	0.954	-0.07	0.528	0.27	*0.043
Change in reach depth	-0.02	0.730	-0.02	0.842	0	0.754	-0.07	0.540	0.27	*0.046
Change in EIV - temperature	-0.02	0.719	-0.05	0.694	0.32	***<0.001	0.05	0.650	-0.26	0.055
Change in EIV - soil reaction	-0.06	0.280	-0.08	0.514	0.21	*0.031	-0.11	0.305	-0.26	0.050
Change in EIV - nutrients	0.09	0.126	-0.03	0.788	0.42	***<0.001	-0.01	0.909	-0.03	0.808

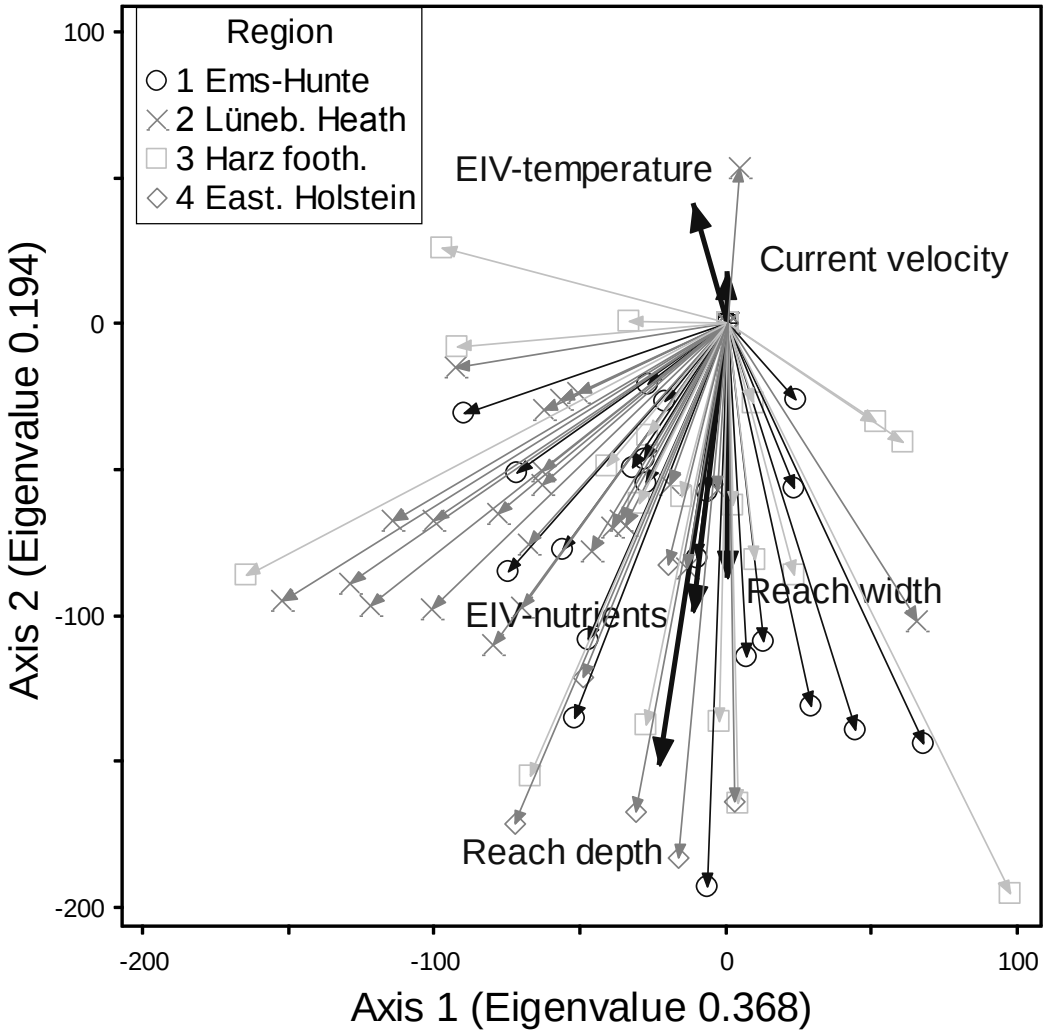


Figure 4.6 Successional vectors translated to origin (1950s) of the summarized relevés for each of the 70 streams or rivers in the four studied regions (thin arrows, 1950s – 2010/2011 contrast) together with environmental variables (thick arrows). See Table 4.7 in the Appendix and Table 4.8 for correlations of the DCA axes and successional vectors with environmental factors

Table 4.8 Correlation coefficients after Spearman and p values of the relationships between environmental variables (changes over time per running water) and the successional vector lengths for 70 streams or rivers, differentiated after regions

Parameter	All regions	p	Region 1	p	Region 2	p	Region 3	p	Region 4	p
Change in current velocity	-0.15	0.350	0.20	0.470	0.11	0.680	-0.10	0.873	-0.37	0.468
Change in reach width	0.27	0.103	0.14	0.642	0.14	0.628	-0.40	0.600	-0.26	0.623
Change in reach depth	-0.24	0.121	-0.17	0.531	-0.16	0.576	-0.30	0.624	-0.49	0.329
Change in EIV - temperature	0.06	0.607	-0.26	0.259	0.35	0.085	0.07	0.761	0.6	0.208
Change in EIV - soil reaction	0.22	0.064	0.18	0.437	0.29	0.161	0.03	0.917	0.6	0.208
Change in EIV - nutrients	0.36	**0.002	0.46	*0.035	0.42	*0.038	0.34	0.158	0.43	0.397

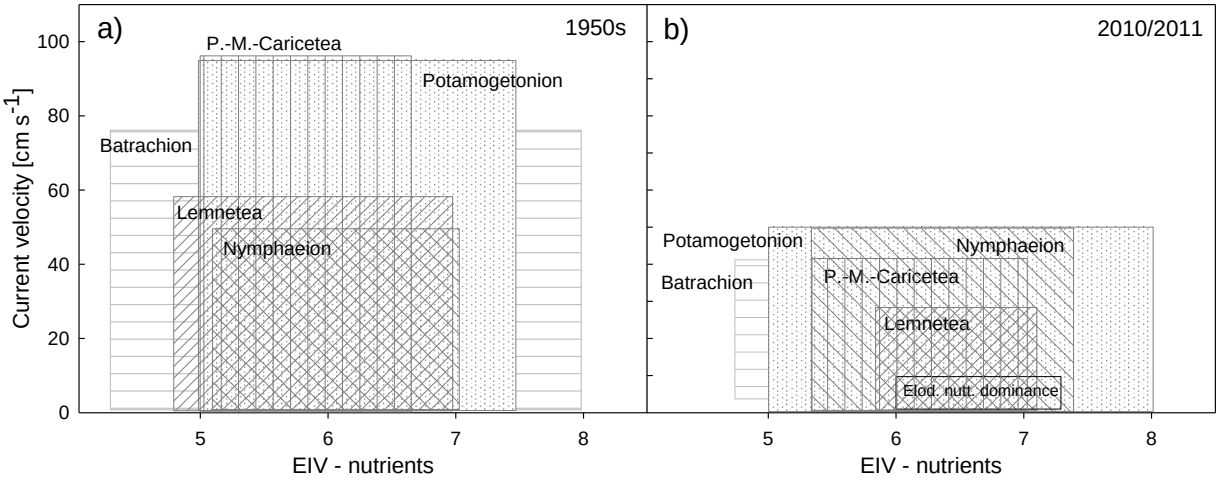


Figure 4.7 Ecograms with the two environmental axes current velocity and Ellenberg indicator value for nutrients plotted for (a) five vegetation units classified after Chytrý (2011) in the 1950s and (b) in 2010/2011 (in 2010/2011, *Elodea nuttallii* dominance stands were additionally plotted)

Discussion

Weaknesses and strengths of the sampling and classification approaches

The sampling and classification of river macrophyte vegetation is associated with a number of problems that relate to the biology of the macrophyte flora, the linear structure of the ecosystem with steep environmental gradients from the river bank to the stream line, and the high dynamics of the assemblages (Mitchell & Rodgers 1986, Boschilia et al. 2008, Haury & Muller 2008). In running waters, stochastic events are more important than in stagnant waters, many taxa are highly plastic, and species richness is typically relatively low (Gessner 1955, Haslam 1987). Most historical vegetation relevés in European inland waters were taken in the tradition of the Zürich-Montpellier school of vegetation science with small plot sizes (typically < 30 m^2) and preferential selection of vegetation stands with presence of diagnostic species. Such an approach may overestimate mean species richness and might be biased in terms of representativeness of community composition and structure. For the sake of comparability, we took the recent relevés as close as possible to the historical sites and also selected the precise plot location preferentially in the same manner as six decades ago. The classification of the relevé material also requires taking subjective decisions in the analysis and different classification systems necessarily lead to partly deviating results.

Our study aim was not to assess the goodness of the two applied classifications, but we asked what information can be gained from these classifications about the fundamental change having taken place in macrophyte community structure and vegetation patterns in the past decades. We assumed that two independent classification systems should lead to more robust conclusions on vegetation change than one system alone. While hierarchical

phytosociological classification concepts are somewhat artificial, such approaches have the advantage that they can also provide information on community impoverishment and community homogenization over time. The phytosociological analysis of the relevé material from the 1950s and 2010/2011 after Preising et al. (1990) showed a large decrease in the proportion of relevés that could be assigned to the association level, indicating losses in characteristic taxa. The decline in phytosociological character species gives reason to assume that many of the syntaxonomic units that were described for north-west German water courses in the past decades do not represent recognizable types of macrophyte assemblages with sufficient homogeneity and wider distribution anymore. However, the possibility of assigning relevés with different degrees of impoverishment to different levels in the syntaxonomic hierarchy may represent a strength of this approach when community change is to be examined. In the classification system of Chytrý (2011), dominance structures are decisive for classification and due to the prevalence of mono-dominant stands, the number of macrophyte associations identified in our study regions (1950s: 29, 2010/2011: 23) was much greater than with the Preising system. For the assessment of change at the community level, it can be viewed as an advantage of this system that every relevé can be assigned unambiguously to a certain association.

Landscape-scale diversity of macrophyte assemblages in historical and recent time

With a macrophyte flora (vascular plants and mosses) of roughly 80 hydro- and amphiphytic or helophytic taxa, the species pool in the streams and rivers of the north-west German lowlands is relatively small. One reason is the rather restricted habitat diversity in the water courses of this landscape that was formed by the penultimate and last Ice Ages and is harboring predominantly potamal streams and rivers with relatively low current velocity. Only very few water courses of the Central German uplands were included in the study and thus, rhithral streams are present only in the study regions 2 (Lüneburg Heath) and 3 (northern Harz foothills) with a more or less undulating relief. Characteristic for the macrophyte vegetation of the north-west German lowlands are submerged assemblages with taxa such as *Myriophyllum alterniflorum* or *Ranunculus fluitans*, which in a number of phytosociological systems (e.g. Preising et al. 1990, Rennwald 2000, Berg et al. 2004) are classified in the Callitricho-Batrachietalia order (class Potamogetonetea), that comprises the largest part of Europe's macrophyte vegetation in lotic waters. These (at least in former times) relatively species-rich assemblages are completed by communities assignable to two other Potamogetonetea orders with mostly species-poor communities, the pondweed assemblages (Potamogetonetalia with three alliances) and the water lily assemblages (Nymphaeetalia with two alliances). Less than 15 percent of the relevés were assigned to

other vegetation classes than the Potamogetonetea (Lemnetea, Phragmitetea/Phragmito-Magno-Caricetea, Platyhypnidio-Fontinalietea antipyreticae).

Following Preising et al. (1990), the phytosociological analysis revealed the presence of 3 orders, 6 alliances and 6 associations within the Potamogetonetea, the 'core class' of macrophyte vegetation. The single most widespread alliance was the Ranunculion fluitantis with its quantitatively most important association, the Callitricho-Myriophylletum. According to their distribution and apparent site preferences, the six Potamogetonetea associations currently present in the study regions according to the Preising system can be characterized as follows:

(1) the Callitricho-Myriophylletum showed a preference for relatively fast-flowing, cool, but nutrient-poor streams and small rivers on base-poor glacial deposits (characteristic for the rhithral waters in particular of the outwash plains of the Lüneburg Heath and its surroundings);

(2) the Ranunculo-Sietum preferred relatively slow-flowing, cool, but base-rich water courses (mainly in waters originating in the loess deposits of the northern Harz foothills);

(3) the Ranunculetum fluitantis was mainly found in relatively fast-flowing, relatively warm and nutrient-enriched water courses (in regions with higher relief energy: Harz foothills, Lüneburg Heath);

(4) the Potamogetonetum lucentis inhabited slowly to faster flowing, relatively eutrophic, potamal river reaches (mainly in the Ems-Hunte and eastern Holstein regions);

(5) the Sparganio-Elodeetum colonizes relatively slow-flowing, moderately nutrient-rich water courses in the base-poor glacial deposits of the Ems-Hunte moraine country; and

(6) the Myriophyllo-Nupharetum is characteristic for relatively warm, nearly stagnant, meso- to eutrophic, potamal water courses (mainly in the Ems-Hunte and Harz foothills regions). The latter assemblage was often associated with lemnid carpets, in particular in the 2010/2011 survey.

Comparing the 1950s data with the recent survey reveals not only a markedly reduced mean species richness of the assemblages (from 4.7 to 3.8 species per relevé, Steffen et al. 2013), but also profound change in the relative abundance of the assemblages in the four study regions. In addition, a general reduction in community diversity at the landscape scale was recognized. Four of the six Potamogetonetea associations assigned after Preising et al. (1990) suffered severe frequency losses (by 30 to 78 %) in the each ~330 relevés between the 1950s and 2010/2011 with large reductions also observed in the once most widespread associations Callitricho-Myriophylletum and Potamogetonetum lucentis. Two types of assemblages, which were in the 1950s assigned to the Potamogetonion graminei and the Hydrocharition, were no longer present in 2010/2011. On the other hand, assemblages assignable to the alliance Nymphaeion albae (and order Nymphaeetalia,

+47 %), i.e. communities dominated by floating-leaved, rooted macrophytes, and lemnid carpets (class Lemnetea) that often occurred together with *Sagittaria sagittifolia*, are much more widespread in recent time than 60 years ago. A large spread was observed in particular for the Nymphaeion association Sparganio-Elodeetum, which roughly doubled the number of its occurrences. This impressive shift from Potamogetonetalia (and Batrachietalia) communities to Nymphaeetalia communities was overlain by a general impoverishment of the assemblages at the plot level, many of which lost their indicative species. Today, only two associations of the phytosociological system of Preising et al. (1990) (Callitricho-Myriophylletum and Sparganio-Elodeetum) can be considered as being more widespread.

When applying the alternative classification system after Chytrý (2011), which puts more weight on dominance relations than on the presence/absence of diagnostic species, the relevés were assigned to 3 Potamogetonetea alliances with 30 associations. According to this classification, the Potamogetonion was the most common alliance, but on the association level, the Nymphaeo albae-Nupharetum luteae (alliance Nymphaeion) and the Callitricho hamulatae-Ranunculetum fluitantis (Batrachion) prevailed. Both classification approaches revealed that Nymphaeetalia/Nymphaeion stands have gained importance during the last 60 years at the expense of Batrachietalia/Batrachion and Potamogetonetalia/Potamogetonion assemblages.

With the reduction in plot-level species richness, the macrophyte assemblages have become more similar to each other resulting in the increase of the average B_{SC} index. The homogenization of river macrophyte vegetation from the 1950s to 2010/2011 is also demonstrated by Figure 4.6 showing a reduction in niche space (current velocity vs. nutrient availability) occupied by the assemblages in recent time. One consequence is the apparent larger overlap of the niches of the different vegetation units in 2010/2011, which relates to the species loss. Most of the species that were lost from the regional species pool of north-west German running waters over the past 60 years are taxa with relatively narrow ecological niches that often served as character species for the syntaxonomic units at lower levels. The large frequency increase in assemblages assignable only to the alliance or order levels after Preising et al. (1990) (by 15 and 62 %, respectively) evidences that many macrophyte stands must be considered as impoverished ‘residual communities’ (Fragmentgesellschaften) in the sense of Brun-Hool (1966) in our times. The fate of the north-west German river macrophyte vegetation since the 1950s is paralleled by the development in terrestrial vegetation types of the cultural landscape of Central Europe, notably the arable field vegetation (Meyer et al. 2010) and the vegetation of managed grasslands (Wesche et al. 2012).

Drivers of community change

The likely main causes of macrophyte community impoverishment and vegetation homogenization at the landscape level are river construction works and eutrophication (Phillips et al. 1978, Pedersen et al. 2006). In north-west Germany, many water courses were straightened and deepened in the course of agricultural intensification to increase run-off, mostly in the 1950s to 1970s. This resulted in the loss of natural floodplain areas with the typical mosaic of side arms, smaller and larger, partly stagnant water bodies, and swamps adjacent to the main rivers. Drag-sensitive species such as *Nymphaea alba* and *Ranunculus circinatus* lost their sheltered habitats and are no longer elements of the macrophyte vegetation of these running waters in recent time. Although our data indicate that many of the investigated water courses were broadened and deepened in the course of engineering works in the last decades especially in the regions 1 (Ems-Hunte) and 4 (eastern Holstein), current velocity seems to be lower in general than in historical time. In principal, a "rhithralization" (more rapid discharge, change to rhithral biotic communities) can be expected as a consequence of river engineering measures (Moog 2002). In our regions, in contrast, a "potamalization" (reduction of the current velocity, change to potamal biota) has taken place after water course regulation, which likely results from the construction of barrages and weirs in many water courses that increased the water level and reduced flow. The correlation of the plot-wise successional vectors for region 4 with increased reach widths and depths indicates a direct relation of the vegetation change in eastern Holstein with river engineering works.

The maintenance of water courses is a legal duty in the study region since 1957 resulting in regular dredging and mowing of most streams and rivers and their banks, thereby eliminating many disturbance-sensitive species. Species with deeper anchoring in the sediment such as *Sagittaria sagittifolia* or *Sparganium emersum* may then profit from reduced competition. Maintenance works also increase the load of suspended particles reducing light transmissivity in the water body (Altmüller & Dettmer 1996). This effect adds to the eutrophication-caused increase in phytoplankton density, which also increases turbidity favoring surface-floating species such as lemnids and nymphaeids over submerged growth forms (Hough et al. 1989). Increasing importance of surface-floating species but declines of rooted, submerged macrophytes has also been observed over the past decades in Dutch streams and was related to eutrophication and increased water turbidity (Mesters 1995). In north-west Germany, agricultural intensification with high inputs of N and P into the water courses proceeded more rapidly in the regions 1, 3 and 4 than in region 2 (Lüneburg Heath) and took place mainly in the 1960s to 1980s (Behrendt et al. 1999). The Lüneburg Heath with its extended forests and, at least in some parts, less-intense agriculture has preserved richer macrophyte vegetation in the streams and rivers; this was already recognized by Herr

et al. (1990). Nevertheless, the correlation of the successional vectors with increased mean EIVs for temperature, soil reaction and nutrients in the study region 2 hints at a strong influence of physico-chemical factors on macrophyte vegetation change in the water courses of the Lüneburg Heath region, where the running waters have less been impacted by construction works since the 1950s. While the amount of P fertilizer used on Germany's farmland peaked in the 1970s and declined recently to the level of the 1950s, N fertilizer input remained four times higher than 60 years ago (Statistisches Bundesamt 2012). Besides the suppression of light-demanding submersed plants, eutrophication is likely the main driver behind the frequency increase in the eutraphent assemblage Sparganio-Elodeetum since the 1950s. Moreover, the mean EIV for nutrients has significantly increased in this assemblage and in the Myriophyllo-Nupharetum (and seems to have increased in three other associations as well) indicating within-community shifts in species composition towards more nutrient-demanding taxa such as the eutraphent neophyte *Elodea nuttallii* and increased abundances of *Myriophyllum spicatum, Lemna minor* and *Spirodela polyrhiza*.

The characteristic species of the Potamogetonetum lucentis in the system of Preising et al. (1990), *Potamogeton lucens* and *P. perfoliatus*, are known to occur in meso- and also eutrophic waters, but are not very tolerant to pollution or highly eutrophic to hypertrophic conditions (Casper & Krausch 1980, Berg et al. 2004). A decline of species of the genus *Potamogeton* in running waters over several decades has been reported by various earlier studies and was attributed to changes in physical and chemical habitat conditions (Grube 1975, Wiegleb et al. 1991, Riis & Sand-Jensen 2001). Due to their potamid growth form with predominant formation of submerged leaves, many *Potamogeton* species are largely dependent on effective light transmission through the water column and thus are sensitive to turbidity and high loads of suspended particles (Heegaard et al. 2001, Garniel 2008). In contrast, the Nymphaeion albae character species *Nuphar lutea* is relatively tolerant towards turbidity and also drag due to its ability to form both submerged and floating leaves (Berg et al. 2004, Bal et al. 2011).

Conclusions

The macrophyte vegetation of north-west German running waters has undergone profound change in the last sixty years, which affected the species composition, plot-level diversity, the regional species pools, and the relative abundance of community types at the landscape level. Despite important regional differences in the development, a similar principal trend was detected in all four study regions suggesting that our results may be valid for the larger part of northern Central Europe. Species lost were mainly specialist taxa with high affinity to certain macrophyte assemblages. This highlights the value of indicator species-based classification systems with small plot sizes for detecting community- and landscape-level vegetation change in running waters. Despite considerable conceptual differences between the two used classification approaches, both analyses revealed a major vegetation shift from prevailing submerged rooted to floating-leaved rooted and lemnid macrophytes. The hierarchical phytosociological system bears the potential of estimating the degree of anthropogenic community impoverishment. Four of the six Potamogetonetea associations after Preising et al. (1990) have markedly decreased since the 1950s, other assemblages have disappeared completely, which urgently demands for more effective conservation and restoration measures in running waters.

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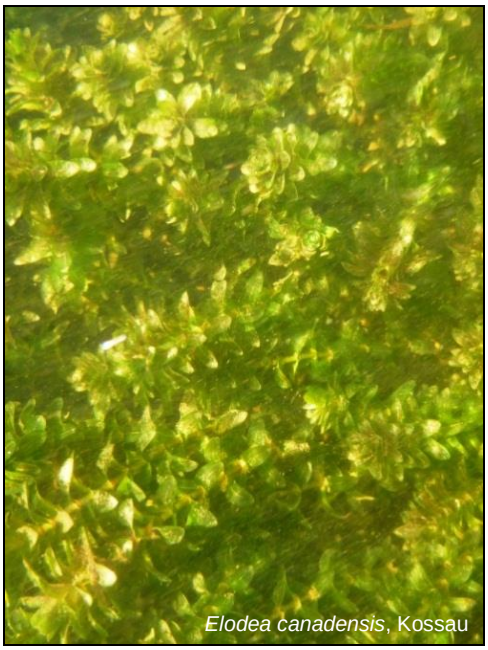
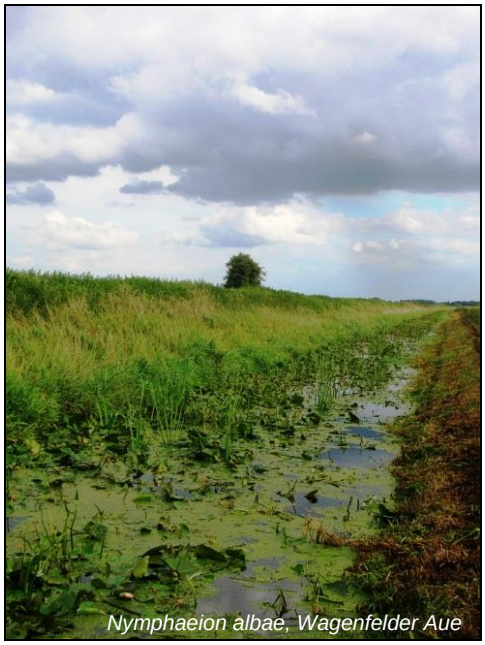
Chapter 5

Synthesis


Elodea canadensis, Kossau


Ranunculion fluitantis, Aschau


Nymphaeion albae, Wagenfelder Aue


Callitriche x vigens, Aller

Methodological remarks: assessing long-term vegetation change in running waters with regard to bioindication

Since the investigation of vegetation change in running waters bases on historical vegetation records with sufficient precision (species lists, cover values), the water courses coming into question for investigation are determined by the historical data available. From the experience of this study, the semi-permanent plot approach bears the potential to take account of the following aspects of aquatic vegetation, which can be considered as very useful to assess long-term changes in running waters:

1. **The species composition**

Due to the differing ecological preferences of different macrophyte species, their presence may be of indicative value. In this regard, the occurrences of stenoecious species as for example *Myriophyllum alterniflorum* preferring mesotrophic, rhithral waters are more meaningful than that of eurioecious ones as for example *Sparganium emersum* occurring under wide amplitudes of currents and trophic conditions. In this study, for example species with broad ecological tolerances and species preferring eutrophic habitats showed an increase over six decades, while mesotrophic species decreased and oligotrophic species died out. This development in the species composition hints at the anthropogenically induced eutrophication of the investigated running waters.

2. **The species richness and diversity**

The size of the species pool reflects the degree of habitat heterogeneity: the more heterogeneous the occurring habitats are, the more species can be present. The diversity and number of species per plot is to be seen in relation to stress and disturbance. In stressful environments or highly disturbed habitats, only a low number of species is able to persist within a defined area. In our example, the species pool as well as plot-level species richness and diversity decreased over the investigated time span. The losses are attributed to habitat uniformization, increased mechanical stress (loss of low-flow and stagnant water habitats that were part of the historical running waters) and regular disturbance (e.g. maintenance works) that occurred in north-west German streams and rivers in the last decades.

3. **The shares of life form (rooted vs. free-floating) and growth form (totally submerged vs. floating-leaved) types**

Rhizophytic, submerged growth forms (e.g. potamid species) depend on relatively clear water with sufficient light transmission through the water column and such are typical for oligo- to moderately eutrophic water bodies. In contrast, pleustophytic growth forms (e.g. lemnid) are also able to colonize highly eu- to hypertrophic, turbid waters. In the water courses we looked at, a shift from the predominance of potamid to the predominance of lemnid species was observed, hinting at an increase in the productivity (eutrophication).

4. **The mean specific leaf area (SLA)**

The mean SLA (i.e. leaf surface area per 1g leaf) of the macrophyte species characterizes their mechanical resistance: less resistant plants have a higher SLA (due to leaves being thin or rich in aerenchymatic tissue). In this study, the mean SLA per plot decreased over 60 years (only hydrophytes were considered), indicating an increase of robust plant species and thus increased mechanical disturbance, which can be related to the loss of sheltered habitats at the edges of the main river channels.

5. **The proportions of syntaxonomic vegetation units as related to different hierarchical levels (class, order, alliance, association)**

To assess the long-term development of the vegetation community structure, it is necessary to classify the documented species assemblages. To detect differences between historical and recent macrophyte assemblages, the syntaxonomic character and/or dominant species-based classifications proved to be appropriate, because they provide the opportunity to quantify the changes at the community level. After the system of Preising et al. (1990), in the vegetation stands that we looked at, the number of phytosociologically well characterized communities (associations) declined over six decades (-26.8 %), while the proportion of assemblages poorly defined by character species (orders, alliances) strongly increased (+14.8–61.7 %). Following Chytrý's (2011) system, with the possibility to assign every stand to an association, the number of recognized associations declined from 29 (1950s) to 23 (2010/2011). The apparent diversity decline at the community level is a sign for habitat homogenization in the investigated running waters.

Vegetation and environmental change in streams and rivers in north-west Germany since the 1950s

The hydrophytic flora of north-west German streams and rivers became impoverished between the 1950s and 2010. The magnitude of change with a reduction of the species pool by 27.5 %, accompanied by a degradation on the syntaxonomic level and a profound shift from the predominance of submerged rhizophytic (mainly potamid) species in the relevés to the predominance of pleustophytic (mainly lemnid) species, is alarming. Looking at the species with considerable changes in their frequencies of occurrence in the study sites over the last six decades, it is evident that oligo- and mesotrophic species such as the character species of the Potamogetonion graminei (e.g. *Potamogeton alpinus*) and of the Callitricho-Myriophylletum (e.g. *Myriophyllum alterniflorum*) have declined or died out, while eutrophic and generalist species such as the character species within the Lemnion gibbae (*Lemna gibba*, *Spirodela polyrhiza*) have increased (Table 5.1). This development corresponds to the increase in the mean EIV for nutrients.

Table 5.1 Changes in the frequency of occurrence between the 1950s and 2010/2011, habitat preferences and syntaxonomic ascription after Preising et al. (1990) of 40 macrophyte species in 338 semi-permanent plots in running waters with a minimum of 3 occurrences in one of the two investigated time periods. (oligo = oligotraphent, meso = mesotraphent, eu = eutraphent, in = indifferent with regard to the nutrient content of the water; (c) = character species for the vegetation unit indicated, (d) = differential species)

Hydrophytic taxon	Occurrences		Change	Ecological preference	Syntaxonomic vegetation unit
	1950s	2010/ 2011	[%]		
Myriophyllum spicatum	3	19	+>100.0	eu [1,7] / in [3]	Potamogetonion lucentis (c)
Utricularia vulgaris	2	10	+>100.0	meso–eu [3,4]	**Nymphaeetalia** (c)
Spirodela polyrhiza	36	110	+>100.0	eu [1] / in [5]	*Spirodeletum polyrhizae* (c)
Elodea nuttallii	0	67	+100.0	eu [1,2]	Potamogetonion pusilli (c)
Lemna minor	115	207	+80.0	in [2,5]	LEMNETEA (c)
Ranunculus trichophyllus	4	7	+75.0	meso–eu [3] / in [5,7]	*Ranunculo-Sietum* (c)
Potamogeton nodosus	2	3	+50.0	in [6]	Ranunculion fluitantis (c)
Lemna gibba	24	33	+37.5	eu [2,5]	*Lemnetum gibbae* (c)
Ceratophyllum demersum	20	24	+20.0	eu [5] / in [7]	POTAMETEA (c)
Hydrocharis morsus-ranae	8	9	+12.5	meso–eu [2,5]	Hydrocharition (c)
Sparganium emersum	176	176	±0.0	in [4,5]	*Sparganio-Elodeetum* (c), Ranunculion fluitantis (d)
Sagittaria sagittifolia	92	85	-7.6	eu [5]	*Sparganio-Elodeetum* (c)
Callitriche palustris agg.	144	122	-15.3	meso–eu [3] / in [4]	*Sparganio-Elodeetum* (c), **Callitricho-Batrachietalia** (c)
Nuphar lutea	117	81	-30.8	in [5]	*Myriophyllo-Nupharetum* (c)
Potamogeton pectinatus	54	35	-35.2	eu [5] / in [6,7]	**Potamogetonetalia** (c), Nymphaeion albae (d)
Lemna trisulca	51	32	-37.3	meso–eu [2]	*Lemnetum trisulcae* (c)
Callitriche hamulata	78	41	-47.4	meso [1,2]	*Callitricho-Myriophylletum* (c)
Potamogeton pusillus	23	12	-47.8	meso–eu [2,5]	Potamogetonion pusilli (c)
Elodea canadensis	135	69	-48.9	eu [2] / in [5]	POTAMOGETONETEA (c)
Fontinalis antipyretica	23	11	-52.2	in [7]	Ranunculion fluitantis (c)
Myriophyllum alterniflorum	32	15	-53.1	meso [1,3]	*Callitricho-Myriophylletum* (d)
Potamogeton crispus	62	25	-59.7	(meso–)eu [5,6] / in [7]	POTAMOGETONETEA (c)
Ranunculus fluitans	16	6	-62.5	eu [4,7]	*Ranunculetum fluitantis* (c)
Ranunculus aquatilis agg.	80	30	-62.5	meso [1,4] / eu [3]	Ranunculion fluitantis (c), *Callitricho-Myriophylletum* (d)
Potamogeton natans	103	35	-66.0	±meso [2] / eu [5]	POTAMOGETONETEA (c)
Myriophyllum verticillatum	3	1	-66.7	meso–eu [3,4]	**Nymphaeetalia** (c)
Potamogeton berchtoldii	3	1	-66.7	meso–eu [2,5]	**Potamogetonetalia** (c)
Potamogeton lucens	37	10	-73.0	meso–eu [7]	*Potamogetonetum lucentis* (c), Nymphaeion albae (d)
Callitriche hermaphroditica	4	1	-75.0	oligo–meso [3]	-
Isolepis fluitans	4	1	-75.0	oligo–meso [2]	-
Potamogeton perfoliatus	42	10	-76.2	meso–eu [2,6]	*Potamogetonetum lucentis* (c), Nymphaeion albae (d)
Zannichellia palustris	14	3	-78.6	eu [5,7]	*Ranunculo-Sietum* (d)
Hippuris vulgaris	3	0	-100.0	meso(–eu) [3,7]	*Ranunculo-Sietum* (d)
Potamogeton compressus	3	0	-100.0	±eu [2,4,5]	**Potamogetonetalia** (c)
Nymphaea alba	4	0	-100.0	in [3,4]	*Myriophyllo-Nupharetum* (c)
Ranunculus circinatus	4	0	-100.0	meso–eu [3,5]	Potamogetonion lucentis (c), Nymphaeion albae (d)
Potamogeton obtusifolius	5	0	-100.0	meso [2,6]	Potamogetonion graminei (c)
Juncus bulbosus fluitans	9	0	-100.0	oligo [2]	Potamogetonion graminei (d)
Potamogeton alpinus	18	0	-100.0	±meso [3,5]	Potamogetonion graminei (c), *Callitricho-Myriophylletum* (d)
Potamogeton friesii	32	0	-100.0	meso–eu [2,6]	Potamogetonion pusilli (c)

[1] based on own observation (see chapter 2), [2] Casper & Krausch (1980), [3] Casper & Krausch (1981), [4] Garniel (2008), [5] Tiedemann (1982), [6] Preston (1995), [7] Kutscher (1984)

The diversity decline in the macrophyte vegetation of north-west German streams and rivers over the last six decades is paralleled by global losses in the diversity of species in rivers (Millennium Ecosystem Assessment 2005), losses in the phytodiversity of European surface waters (e.g. Sand-Jensen et al. 2000, Schütz et al. 2008, Gołdyn 2010) and terrestrial systems in northern Germany (Meyer et al. 2010, Wesche et al. 2012, Leuschner et al. 2013). These studies identify eutrophication as one of the main drivers of vegetation change in the cultural landscapes since the 1950s. Since the 1980s, the nutrient status of the running waters of north-west Germany shows some improvement with more or less significant reductions in the nitrogen and phosphorus loads (Schulz 1999, Behrendt et al. 2002). These more recent developments might be reflected in the slight decrease in the EIV for nutrients since the 1980s; it appears that the vegetation is responding only slowly to the achievements.

The fact that current-intolerant species (*Nymphaea alba*, *Ranunculus circinatus*) could no longer be found in the investigated water courses in 2010/2011 indicates that sheltered inlets and small bays with calm water have disappeared, thus hinting at structural impoverishment of the riverbeds. The decline in plot-level species richness and diversity is assumed to be a consequence of increased disturbance, for example by construction or maintenance works. Increased disturbance is also indicated by the relative increase in summergreen species (including the lemnids and some nymphaeids) with the concurrent decline in evergreen species (the batrachids and most potamids), by the increase in R-strategists, as well as by the decrease in the mean SLA over the last six decades. Supporting this, Baattrup-Pedersen et al. (2002) found a higher proportion of R-strategists and a lower species richness and diversity in reaches, where weed-cutting is practiced when comparing weed-cut and uncut stream reaches.

Future outlook

The effects of climatic change can hardly be predicted. Warmer winters will probably favour the arrival of alien species, altering aquatic communities. In an artificially warmed river in North Rhine-Westphalia, a number of neophytic species became established and seems to be an addition to the local species pool, without causing harm to the native flora (Hussner & Lösch 2005). Experiments by Mckee et al. (2002) showed that the exotic macrophyte *Lagarosiphon major* profited more from an increased water temperature than species established in Britain. Phytoplankton and algal growth might also be enhanced by warmer temperatures. Alahuhta et al. (2011) speculated referring to a modelling study for Finland that at higher temperatures emergent macrophytes might in many cases overgrow submerged vegetation. Elevated carbon dioxide concentrations might also favour

macrophytes that are not capable of using bicarbonate as a carbon source (Johnson et al. 2009) such as for example *Fontinalis antipyretica* (Gessner 1959).

To reverse the diversity decline in river macrophytes, the homogenization of their habitats has to be reversed. Renaturalization measures aiming at the recreation of richly structured water courses with meanders, side arms, sheltered bays and shallow transition zones to floodplain areas need to go hand in hand with continuing efforts to reduce the nutrient inflows from the catchments. An extensive management of low-lying farmland renders intensive drainage and maintenance of the water courses unnecessary. Weed-cutting may be minimized and carried out in a gentle manner for example with a mowing bucket at ecologically sound dates (in autumn after fruit formation). Eutrophication can only be controlled if both, nitrogen and phosphorus inputs are reduced, considering also that phosphorus depositions may be stored in anoxic sediments as “internal loading” for decades (Conley et al. 2009) and that nitrogen has residence times of up to 30 years in the groundwater (Umweltbundesamt 2013). Impacts from intensive land use would in some cases be reduced if riparian buffer strips of at least 5 m width were established (Gunkel 1996). Jahn & Dembinski (2000) estimated costs for the revitalization of two small rivers in Lower Saxony and arrived at 23,000–33,000 € km^{-1} mainly accounting for land extensification and also for the regeneration of a natural riverbed morphology to restore natural runoff dynamics.

In this way, specialist and less robust species, having once been much more abundant in north-west German running waters, might be able to become more distributed again. The re-establishment of locally extinct macrophyte species in suitable habitats is possible by reintroducing plants preferably from autochthonous populations (Kaplan et al. 1998), also paying attention to natural growth areas as for example the Ranunculo-Sietum community being typical for rhithral reaches and the Potamogetonetum lucentis growing in more or less potamal reaches. Regeneration processes like this cannot be expected to take less time than the decades of decrease took. In streams of the Donau catchment in southern Germany, an improvement in the water quality of a reach formerly influenced by sewage discharge was reflected in the macrophyte vegetation only after 15 years (Veit & Kohler 2003). Conserving the phytodiversity of streams and rivers is essential to keep the ecosystems functioning, not least for the benefit of humans.

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Appendix

Table 2.2 Affinity of the 31 most abundant macrophyte species to 28 physical, chemical or river morphological parameters. Indicated are environmental parameters with significantly higher value (black fields) or significantly lower value (white fields) in plots with presence of the target species than in plots with the species' absence. Grey field = no significant difference between habitats with and without the species, * = p<0.05, ** = p<0.01, *** = p<0.001. Figures give the mean of the variable for all plots with the species' presence. Wat. = Water, Sed. = Sediment

Macrophyte species (no. of plots)	Current velocity [cm s^{-1}]	Depth [m]	Anthrop. influence	Wat. pH	Sed. pH	Sed. C_{tot} [mmol/g]	Sed. C_{org} [mmol/g]	Wat. NH_4 [mg/l]	Wat. NO_3 [mg/l]	Sed. N_{tot} [mmol/g]	Sed. C/N ratio	Sed. N/P ratio	Wat. PO_4 [mg/l]	Sed. P_{resin} [µmol/g]
Myri. alte. (16)	** 17.5		** 2.9		** 6.7	** 0.53	** 0.47	** 0.03		* 0.06			* 0.01	** 1.67
Ranu. pelt. (28)		* 0.6	** 3.1		** 6.8									*** 2.24
Call. hamu.(42)		** 0.8	*** 3.0		*** 6.7			** 0.08	** 2.91				* 0.02	*** 3.70
Beru. erec. (57)	** 17.4	*** 0.6	*** 3.0		** 7.0		** 1.71	*** 0.06		** 0.12	** 10.35			*** 3.02
Glyc. flui. (24)		*** 0.4	*** 2.9		*** 6.6									
Font. anti. (20)	** 18.9	*** 0.8	* 3.2					* 0.07	** 3.45	* 0.13				* 2.54
Spar. erec. (90)					* 7.2									
Elod. cana. (71)														
Call. obtu. (12)								* 0.31						* 7.22
Call. plat. (108)			** 3.3					*** 0.24				* 88.32		
Phal. arun. (161)														
Phra. aust. (26)			*** 2.95					** 0.10						
Pota. perf. (12)														
Pota. pusi. (10)														
Pota. nata. (36)			*** 3.5	* 8.0		* 2.04	* 1.98	*** 0.28	** 1.73		* 13.56	* 136.01		
Utri. vulg. (10)							* 4.38				* 16.89		* <0.01	
Buto. umbe. (35)			** 3.1					** 0.09						
Lemn. tris. (32)														
Pota. pect. (36)			** 3.3	* 8.3				*** 0.08	** 2.76					* 4.51
Pota. luce. (13)	* 7.9													
Lemn. gibb. (31)	** 8.5	* 1.4												
Spar. emer. (169)		*** 1.1	* 3.2					*** 0.15				*** 82.85		
Cera. deme. (23)								* 0.44						
Lemn. mino. (192)		*** 1.1	** 3.3				*** 2.21	*** 0.23	*** 2.12	*** 0.15				*** 5.93
Hydr. mors. (12)	* 7.1	* 1.5			* 7.1			* 0.14	** 1.14				* 0.04	
Pota. cris. (27)		** 1.1						** 0.26	** 2.76					* 0.10
Spir. poly. (107)	*** 8.7	*** 1.3				*** 2.99	*** 2.86	*** 0.31	*** 1.56	*** 0.19	* 13.66	* 235.72		
Elod. nutt. (71)		** 1.4		** 8.3		** 2.98	** 2.85			** 0.19	*** 15.51			* 7.75
Nuph. lute. (93)		*** 1.3	*** 3.4		*** 7.2	** 2.21	** 2.12	*** 0.20	* 1.99	** 0.16		* 61.54		** 7.04
Sagi. sagi. (83)	*** 7.8	*** 1.5	*** 3.6	*** 8.2	*** 7.3			** 0.27				** 171.68	* 0.01	*** 10.11
Myri. spic. (23)		** 1.6			** 7.3			* 0.08	** 3.37					*** 7.59

Table 2.2 continued

Macrophyte species (no. of plots)	Wat. S [mg/l]	Wat. Ca [mg/l]	Sed. Ca [µmol/g]	Wat. Mg [mg/l]	Sed. Mg [µmol/g]	Wat. K [mg/l]	Sed. K [µmol/g]	Wat. Na [mg/l]	Sed. Na [µmol/g]	Sed. CEC [$\mu mol_c/g$]	Wat. Fe [mg/l]	Sed. Fe [µmol/g]	Wat. Al [mg/l]	Sed. Al [µmol/g]
Myri. alte. (16)		* 23.50	** 23.98	*** 5.58	** 2.43		** 0.63		*** 0.80	* 37.97		* 0.41		
Ranu. pelt. (28)		** 15.78	*** 16.80	* 3.09	** 1.48		*** 0.50		** 1.05	* 50.79				** 0.32
Call. hamu.(42)	** 10.35	*** 22.08	*** 32.32	** 4.45	*** 3.04		** 1.09		** 1.46	*** 87.08				*** 0.61
Beru. erec. (57)			** 51.47		** 3.92	* 3.56		* 21.4	** 1.87		** 0.13	** 3.20	* 0.01	* 0.31
Glyc. flui. (24)			** 42.53									*** 0.86		*** 0.97
Font. anti. (20)				* 12.06							** 0.06			
Spar. erec. (90)		** 50.45		* 10.49		* 5.55		* 35.4						
Elod. cana. (71)	* 15.01	* 33.52							* 1.87		* 0.16			
Call. obtu. (12)		* 29.31		* 4.88										
Call. plat. (108)	*** 16.77	*** 33.67		*** 6.93				** 26.2		*** 127.13	** 0.26	** 6.34		** 0.52
Phal. arun. (161)						** 5.68								
Phra. aust. (26)												*** 2.43		
Pota. perf. (12)														
Pota. pusi. (10)											* 1.09			
Pota. nata. (36)			*** 66.08		** 4.47		* 1.28				** 0.43	** 10.60		** 0.25
Utri. vulg. (10)			* 145.27											
Buto. umbe. (35)	*** 27.59	*** 57.01		*** 10.35			* 1.61	* 48.2	* 3.17		* 0.15	** 0.89	* 0.01	* 0.01
Lemn. tris. (32)	** 16.54		* 88.67	* 6.62		** 4.37		* 19.7		* 211.43			* 0.01	
Pota. pect. (36)	*** 45.17	*** 69.44		*** 16.43		*** 7.93		*** 71.0		* 139.43	** 0.13	** 1.04		
Pota. luce. (13)				* 5.09							* 0.21		* <0.01	
Lemn. gibb. (31)	* 24.66				** 5.08	*** 6.64		** 38.4						
Spar. emer. (169)	*** 23.93	*** 42.02		** 9.03					* 2.11	* 119.34	*** 0.17	* 3.81		
Cera. deme. (23)														
Lemn. mino. (192)	*** 20.24	*** 39.59	*** 67.78	*** 8.17	* 4.82			* 30.2			*** 0.22	*** 6.01		
Hydr. mors. (12)				* 6.40									* <0.01	
Pota. cris. (27)	** 34.05	** 56.65		* 11.62						* 162.34	* 0.15	** 1.93		* 0.01
Spir. poly. (107)			*** 87.78								* 0.25	* 7.86		
Elod. nutt. (71)	*** 21.32					*** 5.89	* 1.57	*** 36.5	* 2.49				* <0.01	
Nuph. lute. (93)		* 47.47	*** 69.16		*** 5.03		*** 1.5		** 2.56		** 0.22	*** 6.67	* <0.01	*** 0.08
Sagi. sagi. (83)						*** 5.60		*** 34.2	** 2.58	* 177.75	*** 0.33	*** 10.61		
Myri. spic. (23)	*** 35.20	*** 54.16	** 81.72	*** 10.38	** 7.62		** 2.5	*** 65.3	** 5.07		** 0.09			** 0.02

Table 2.5 Correlations after Spearman of environmental variables with the DCA axes 1 and 2. Only variables correlating at r > ±0.20 with one of the axes are shown. Significance values were not derived from a permutation test and are only indicated as a guidance

Environmental variable	r DCA axis 1	p	r DCA axis 2	p
Depth [m]	-0.60	<0.001	0.02	0.735
Width [m]	-0.49	<0.001	-0.06	0.352
Current vel. [cm s^{-1}]	0.45	<0.001	0.13	0.025
NH_4 (Water)	-0.41	<0.001	0.02	0.776
Anthropogenic influence	-0.37	<0.001	-0.12	0.045
Fe (Water)	-0.36	<0.001	-0.30	<0.001
Na (Water)	-0.34	<0.001	0.04	0.556
P_{resin} (Sediment)	-0.33	<0.001	-0.12	0.041
CEC (Sediment)	-0.32	<0.001	0.15	0.014
Ca (Sediment)	-0.30	<0.001	0.18	0.003
C_{org} (Sediment)	-0.30	<0.001	0.10	0.089
Mn (Water)	-0.30	<0.001	-0.17	0.004
K (Water)	-0.29	<0.001	-0.04	0.531
Fe (Sediment)	-0.28	<0.001	-0.03	0.573
Na (Water)	-0.27	<0.001	-0.02	0.708
K (Sediment)	-0.26	<0.001	0.04	0.482
N (Sediment)	-0.25	<0.001	0.10	0.099
NO_3 (Water)	0.24	<0.001	-0.18	0.002
Mn (Sediment)	-0.23	<0.001	-0.09	0.151
Mg (Sediment)	-0.23	<0.001	0.10	0.088
Zn (Water)	-0.09	0.148	-0.22	<0.001
pH (Sediment)	-0.19	0.002	0.20	<0.001

Table 3.1 Sampled water courses by region and corresponding number of relevés

Region	Catch-ment basins	Streams / rivers	No. of relevés period A and period C	No. of relevés period B
1 Ems-Hunte moraine (western / central Lower Saxony)	Ems, Weser	Bornbach, Bruchgraben, Dadau, Dorflohne, Elze, Ems, Eyter, Flöthe, Grawiede, Grenzkanal, Hase, Hunte, Lohne, Lotterbeke, Mittelradde, Steinhuder Meerbach, Strothe, Schwarze Riede, Uchter Mühlenbach, Wagenfelder Aue	77	45
2 Lüneburg Heath (eastern Lower Saxony)	Weser	Aue, Aschau, (Seehals-) Beeke, Berger Bach, Böhme, Bokeler Bach, Bruchbach, Emmerbach, Ilmenau, Kainbach, Kleine Örtze, Kohlenbach, Knesebach, Lachte, Lutter, Örtze, Schmalwasser, Schwarzwasser, Wiehe, Wietze	86	17
with Aller lowlands (eastern Lower Saxony)	Weser	Aller, Allerkanal, Kleine Aller, Fuhse, Ise, Westaue	23	8
3 Northern Harz foothills (eastern Lower Saxony)	Weser	Altenau, Erse, Fuhse, Ilse, Kanal-Ilse, Lutter (Elm), Oker, Schiffgraben, Schunter, Spring, Wabe, Warne	75	1
with Weser-Leine uplands (southern Lower Saxony, eastern North Rhine-Westphalia)	Rhine, Weser	Beke, Emmer, Glenne, Grone, Liesenbach, Niese, Oder	16	7
4 Eastern Holstein moraine (eastern Schleswig-Holstein)	Baltic Sea	Behler Bach, effluent stream from Stocksee to Nehmter Binnenau, Kossau, Kührener Au, Schwentine, Tensfelder Au	61	22
Total no. of relevés			338	100

Table 3.2 List of all hydrophytic species and related traits. (Strategy type: c = competitor, s = stress strategist, r = ruderal strategist; pollination type: an = anemogamy, au = autogamy, hy = hydrogamy, zo = zoogamy (in = insects, sn = snails); leaf longevity: ev = evergreen, su = summergreen. Red List status in Germany: 2 = endangered, 3 = vulnerable, V = near threatened, G = data missing, but assumed to be vulnerable)

Species	Strategy type (CRS)	Pollination type	Leaf longevity	Red List status
Callitriche hamulata	crs	an, hy, au	ev	–
Callitriche hermaphroditica	–	hy, au	ev	G
Callitriche palustris agg.	–	–	–	–
Ceratophyllum demersum	sss	hy	ev	–
Chiloscyphus polyanthos (liverwort)	–	–	–	–
Elodea canadensis	css	hy	ev	–
Elodea nuttallii	css	hy	ev	–
Fontinalis antipyretica (moss)	–	–	–	V
Groenlandia densa	sss	an, hy, au	su	2
Helosciadium inundatum	css	au, zo (in)	su	2
Hippuris vulgaris	css	an	su	3
Hydrocharis morsus-ranae	css	zo (in)	su	3
Isolepis fluitans	css	an	ev	2
Juncus bulbosus fluitans	crs	an	ev	–
Lemna gibba	rss	an, hy, au, zo (in, sn)	su	–
Lemna minor	rss	an, hy, au, zo (in, sn)	su	–
Lemna trisulca	sss	an, hy, au, zo (in, sn)	su	–
Leptodictyum riparium (moss)	–	–	–	–
Luronium natans	sss	au, zo (in)	ev	2
Myriophyllum alterniflorum	css	an	ev	2
Myriophyllum spicatum	css	an, au, zo (in)	ev	–
Myriophyllum verticillatum	css	an, hy	ev	–
Nuphar lutea	css	zo (in)	su	–
Nymphaea alba	css	au, zo (in)	su	–
Platyhypnidium riparioides (moss)	–	–	–	–
Potamogeton acutifolius	sss	an	ev	3
Potamogeton alpinus	css	an	ev	3
Potamogeton angustifolius	–	–	ev	2
Potamogeton berchtoldii	rss	an, hy	ev	V
Potamogeton compressus	sss	an, hy	ev	2
Potamogeton crispus	css	an	ev	–
Potamogeton filiformis	rss	an, hy, au	ev	2
Potamogeton friesii	sss	an, hy	ev	2
Potamogeton gramineus	css	an, hy	ev	2
Potamogeton lucens	css	an, hy	ev	V
Potamogeton natans	crs	an	ev	–
Potamogeton nodosus	crs	an, hy	ev	V
Potamogeton obtusifolius	sss	an, au	ev	3
Potamogeton pectinatus	rss	an, hy	ev	–
Potamogeton perfoliatus	css	an, hy	ev	V
Potamogeton polygonifolius	crs	an, hy	ev	3

Species	Strategy type (CRS)	Pollination type	Leaf longevity	Red List status
Potamogeton praelongus	css	an, hy	ev	2
Potamogeton pusillus	rss	an, hy	ev	V
Potamogeton trichoides	sss	an, hy	ev	3
Potamogeton crispus x perfoliatus	–	–	–	–
Ranunculus aquatilis agg.	–	–	–	–
Ranunculus circinatus	css	au, zo (in)	ev	V
Ranunculus fluitans	css	au	ev	V
Ranunculus hederaceus	css	au, zo (in)	ev	2
Ranunculus trichophyllus	css	au, zo (in)	ev	V
Sparganium emersum	css	an	ev	–
Sparganium natans	css	an	ev	2
Spirodela polyrhiza	rss	an, hy, au, zo (in, sn)	su	–
Utricularia neglecta	sss	zo (in)	su	3
Utricularia vulgaris	sss	zo (in)	su	3
Wolffia arrhiza	sss	au	su	2
Zannichellia palustris	sss	hy, au	ev	V

Table 3.3 Correlation of time (sampling date), the number of red-listed species per relevé, biotic traits and environmental variables with the DCA axes 1 and 2. The significance levels are not based on a randomization test; they are only given for indicating the strength of the relationships

Variable	Correlation type	r	DCA axis 1	r	DCA axis 2
Time [year]	Spearman	0.03	p=0.665	0.41	p<0.001
Red-listed species / relevé	Spearman	-0.15	p=0.011	-0.45	p<0.001
Pleustophytic [%]	Spearman	-0.44	p<0.001	0.27	p<0.001
Potamid [%]	Spearman	-0.17	p=0.005	-0.53	p<0.001
Batrachid [%]	Pearson	0.49	p=0.001	-0.00	p=0.999
Nymphaeid [%]	Pearson	-0.29	p<0.001	0.05	p=0.531
C-strategists [%]	Pearson	0.33	p<0.001	-0.03	p=0.591
R-strategists [%]	Pearson	-0.17	p=0.010	0.19	p=0.003
S-strategists [%]	Pearson	-0.37	p<0.001	-0.21	p<0.001
Evergreen species [%]	Spearman	0.54	p<0.001	-0.42	p<0.001
SLA [m^2 kg^{-1}]	Pearson	0.21	p<0.001	-0.59	p<0.001
EIV for nitrogen	Pearson	-0.08	p=0.197	-0.20	p<0.001
EIV for soil reaction	Spearman	-0.33	p<0.001	-0.16	p=0.009
EIV for temperature	Pearson	-0.39	p<0.001	-0.04	p=0.534
Current velocity [cm s^{-1}]	Spearman	0.44	p<0.001	-0.25	p<0.001

Table 3.5 Changes in species richness and diversity between the 1950s and 2010/2011

Diversity parameter	1950s	2010/ 2011	Direction of change[1]	Z	p Wilcoxon-test	T	p t-test
Species richness / relevé	4.7	3.8	↓	-5.8	<0.001		
Red-listed species / relevé	0.9	0.3	↓	-8.9	<0.001		
Diversity (D)	2.8	2.3	↓			5.4	<0.001

[1] ↓ = decrease, ↑ = increase

Table 3.7 Changes in proportions of life or growth forms between the 1950s and 2010/2011

Life / growth form	1950s	2010/2011	Change[1]	Z	p Wilcoxon-test
Pleustophytic [%]	15.5	33.8	↑	-8.2	<0.001
Vallisnerid [%]	10.8	18.0	↑	-4.1	<0.001
Bryid [%]	4.3	5.3	-	-0.1	0.924
Myriophyllid [%]	4.3	4.2	-	-0.7	0.477
Elodeid [%]	10.0	9.1	-	-0.2	0.845
Peplid [%]	13.6	11.3	↓	-2.1	0.040
Isoetid [%]	0.4	0.0	↓	-2.7	0.008
Potamid [%]	19.6	7.7	↓	-8.0	<0.001
Batrachid [%]	6.1	2.0	↓	-5.9	<0.001
Nymphaeid [%]	15.3	8.6	↓	-5.9	<0.001

[1] ↓ = decrease, ↑ = increase

Table 3.10 Changes in biological and environmental traits between the 1950s, 1980s and 2010/2011

Parameter	1950s	1980s	2010	Main effect[1]	Change[2] 1950s-1980s	Change[2] 1980s-2010	Change[2] 1950s-2010
Pleustophytic [%]	20.9	26.2	38.7	S <0.001	-	↑ **	↑ ***
Nymphaeid [%]	21.7	16.0	12.7	G <0.001	↓ **	-	↓ ***
Potamid [%]	17.2	16.0	6.1	G <0.001	-	↓ **	↓ ***
Batrachid [%]	5.0	2.3	1.0	G <0.001	↓ *	-	↓ ***
C-strategists [%]	25.2	20.5	17.5	S <0.001	↓ **	↓ *	↓ ***
R-strategists [%]	9.9	14.7	14.9	G 0.010	↑ *	-	↑ **
S-strategists [%]	64.8	64.9	67.6	G 0.010	-	-	↑ **
Anemogamy [%]	39.8	42.7	34.6	S 0.024	-	↓ *	-
Hydrogamy [%]	27.2	23.7	27.6	G 0.416	-	-	-
Autogamy [%]	9.5	9.1	10.0	G 0.479	-	-	-
Zoogamy [%]	24.5	25.2	27.2	G 0.509	-	-	-
Evergreen species [%]	65.8	59.6	48.8	S <0.001	-	↓ *	↓ ***
SLA [m^2 kg^{-1}]	37.2	35.3	28.9	S 0.001	-	↓ **	↓ **
EIV for nitrogen	6.0	6.4	6.3	G <0.001	↑ ***	-	↑ ***
EIV for soil reaction	6.6	6.8	6.6	S <0.001	↑ ***	↓ **	-
EIV for temperature	5.7	5.6	5.7	G 0.061	-	-	-

[1] Main effect: S = sphericity, G = Greenhouse-Geisser, [2] ↓ = decrease, ↑ = increase, * = p<0.05, ** = p<0.01, *** = p<0.001

Table 4.1a Macrophyte vegetation of north-west German running waters in the 1950s as classified after Preising et al. (1990). Relevés assigned to lower syntaxonomic levels than the class belong to several groups; 337 relevés are included. No specific character species is attributed to the Nymphaeion albae, being characterized by differential species. Base figures: relative frequency of species occurrence within a group in percent; exponents: cover values as averages within groups

No. of species / relevé	6.6	6.4	6	5.2	5.2	9.6	6.2	3.5	6.9	7.6	6.7	6.8	6.9	7.2	7.6	5.6	3
No. of relevés	336	59	1	41	40	16	52	2	40	12	24	219	212	95	17	10	1
	Potametea	Potametalia	Potamion graminei	Potamion lucentis	Potametum lucentis	Potamion pusilli	Nymphaeetalia	Hydrocharition	Nymphaeion albae	Myriophyllo-Nupharetum	Sparganio-Elodeetum	Batrachietalia	Ranunculion fluitantis	Callitricho-Myriophylletum	Ranunculo-Sietum	Ranunculetum fluitantis	Phragmitetea
Lemnetea																	
Spirodela polyrhiza	11 [12]	8 [12]	.	10 [11]	10 [11]	6 [15]	31 [10]	.	30 [9]	42 [8]	25 [9]	5 [15]	4 [9]	1 [<1]	.	.	.
Lemna minor	34 [10]	37 [7]	100 [<1]	24 [10]	25 [10]	69 [6]	46 [6]	.	55 [6]	83 [7]	42 [4]	30 [13]	30 [11]	22 [23]	12 [63]	30 [<1]	.
Lemna trisulca	15 [6]	17 [6]	.	20 [5]	20 [5]	13 [8]	33 [6]	.	38 [2]	75 [2]	25 [3]	10 [4]	10 [4]	3 [<1]	.	10 [<1]	.
Lemna gibba	7 [7]	12 [2]	.	.	.	44 [2]	17 [7]	.	20 [8]	42 [<1]	8 [31]	3 [<1]	3 [<1]	.	.	.	.
Potametea																	
Elodea canadensis	40 [17]	34 [18]	.	37 [22]	35 [23]	25 [8]	27 [21]	.	25 [14]	17 [20]	33 [12]	44 [15]	43 [14]	48 [15]	6 [38]	50 [14]	.
Potamogeton natans	31 [14]	54 [12]	100 [15]	37 [12]	38 [12]	100 [13]	58 [15]	50 [3]	68 [15]	83 [12]	54 [19]	19 [14]	19 [14]	7 [14]	6 [3]	10 [1]	.
Potamogeton crispus	18 [8]	27 [1]	.	15 [13]	15 [13]	63 [10]	23 [6]	.	30 [6]	33 [5]	29 [7]	16 [7]	16 [6]	9 [10]	12 [9]	10 [1]	.
Ceratophyllum demersum	6 [12]	8 [2]	.	10 [2]	10 [2]	6 [3]	19 [14]	50 [1]	18 [13]	33 [9]	13 [18]	2 [20]	2 [20]	.	.	10 [63]	.
Persicaria amphibia	2 [5]	3 [8]	.	5 [8]	5 [8]	.	8 [2]	.	8 [3]	25 [3]	.	<1 [3]	.	.	.	.	.
Potametalia																	
Potamogeton acutifolius	.	2 [1]	.	2 [1]	3 [1]	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton berchtoldii	1 [3]	2 [3]	.	.	.	6 [3]	2 [3]	.	3 [3]	.	.	<1 [3]	.	.	.	.	.
Potamogeton compressus	1 [7]	2 [73]	.	2 [15]	3 [15]	.	4 [27]	.	3 [3]	8 [3]	.	.	.	.	.	.	.
Potamogeton pectinatus	16 [24]	24 [19]	.	15 [26]	13 [32]	44 [11]	17 [25]	.	23 [25]	.	25 [22]	14 [25]	15 [25]	1 [15]	.	20 [9]	.
Potamion graminei																	
Potamogeton angustifolius	<1 [63]	.	.	.	.	.	.	.	.	.	.	<1 [63]	.	1 [63]	.	.	.
Potamogeton obtusifolius	1 [11]	3 [1]	.	5 [1]	5 [1]	.	2 [15]	.	.	.	.	1 [19]	1 [19]	.	.	20 [19]	.
Sparganium natans	<1 [3]	2 [3]	100 [3]	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus bulbosus	3 [3]	.	.	.	.	.	.	.	.	.	.	4 [3]	4 [3]	9 [3]	.	.	.
Potamogeton gramineus	<1 [1]	.	.	.	.	.	2 [1]	.	3 [1]	.	4 [1]	.	.	.	.	.	.
Potamion lucentis																	
Myriophyllum spicatum	1 [3]	5 [3]	.	5 [3]	5 [3]	6 [3]	.	.	.	.	.	.	.	.	.	.	.
Ranunculus circinatus	1 [5]	5 [2]	.	7 [2]	5 [3]	.	2 [15]	50 [15]	.	.	.	.	.	.	.	.	.
Potametum lucentis																	
Potamogeton lucens	11 [25]	51 [28]	.	73 [28]	75 [28]	.	4 [39]	.	5 [39]	17 [39]	.	2 [2]	2 [2]	.	.	.	.
Potamogeton perfoliatus	13 [16]	32 [21]	.	46 [21]	48 [21]	.	10 [7]	.	13 [7]	.	17 [9]	8 [13]	8 [14]	3 [18]	.	50 [12]	.

No. of species / relevé	6.6	6.4	6	5.2	5.2	9.6	6.2	3.5	6.9	7.6	6.7	6.8	6.9	7.2	7.6	5.6	3
No. of relevés	336	59	1	41	40	16	52	2	40	12	24	219	212	95	17	10	1
	Potametea	Potametalia	Potamion graminei	Potamion lucentis	Potametum lucentis	Potamion pusilli	Nymphaeetalia	Hydrocharition	Nymphaeion albae	Myriophyllo-Nupharetum	Sparganio-Elodeetum	Batrachietalia	Ranunculion fluitantis	Callitricho-Myriophylletum	Ranunculo-Sietum	Ranunculetum fluitantis	Phragmitetea
Potamion pusilli																	
Potamogeton pusillus	7 [24]	29 [30]	.	5 [2]	5 [2]	94 [33]	4 [26]	.	5 [26]	8 [38]	4 [15]	2 [2]	2 [2]	2 [2]	.	.	.
Potamogeton friesii	10 [12]	25 [21]	.	5 [50]	5 [50]	81 [17]	10 [4]	.	13 [4]	33 [1]	.	5 [3]	6 [3]	2 [2]	.	.	.
Nymphaeetalia																	
Myriophyllum verticillatum	1 [6]	3 [2]	.	5 [2]	5 [2]	.	2 [15]	.	3 [15]	8 [15]	.	.	.	.	.	.	.
Utricularia vulgaris	1 [19]	.	.	.	.	.	4 [19]	50 [38]	3 [1]	.	.	.	.	.	.	.	.
Hydrocharition																	
Hydrocharis morsus-ranae	2 [13]	2 [15]	.	2 [15]	3 [15]	.	8 [18]	100 [20]	5 [15]	17 [15]	.	1 [5]	1 [5]	1 [1]	.	10 [1]	.
Myriophyllo-Nupharetum																	
Nuphar lutea	35 [21]	37 [18]	.	41 [16]	43 [16]	31 [24]	88 [28]	.	95 [30]	100 [48]	92 [22]	22 [15]	21 [16]	11 [6]	6 [1]	20 [44]	.
Nymphaea alba	1 [14]	.	.	.	.	.	8 [14]	.	10 [14]	33 [14]	.	.	.	.	.	.	.
Sparganio-Elodeetum																	
Sagittaria sagittifolia	27 [12]	36 [13]	.	44 [15]	45 [15]	19 [1]	56 [20]	.	68 [20]	25 [7]	96 [23]	19 [7]	20 [7]	13 [3]	.	.	.
Sparganium emersum	52 [19]	36 [16]	.	20 [12]	20 [12]	81 [19]	42 [12]	.	55 [12]	42 [2]	58 [15]	61 [20]	63 [20]	72 [13]	.	60 [23]	.
Batrachietalia																	
Callitriche palustris agg.	42 [7]	27 [4]	.	2 [3]	3 [3]	94 [4]	25 [8]	50 [1]	30 [9]	.	50 [9]	51 [8]	52 [8]	69 [9]	53 [13]	10 [1]	.
Glyceria fluitans	48 [7]	22 [7]	.	24 [8]	25 [8]	19 [2]	4 [3]	.	5 [3]	.	8 [3]	67 [7]	66 [6]	73 [7]	82 [2]	70 [4]	.
Agrostis stolonifera	32 [1]	19 [1]	.	.	.	69 [1]	10 [1]	.	13 [1]	.	17 [1]	42 [1]	43 [1]	42 [1]	82 [3]	.	.
Ranunculion fluitantis																	
Fontinalis antipyretica M	7 [6]	.	.	.	.	.	.	.	.	.	.	11 [6]	11 [6]	16 [7]	.	20 [8]	.
Potamogeton nodosus	1 [63]	.	.	.	.	.	.	.	.	.	.	1 [63]	1 [63]	.	.	.	.
Berula erecta	28 [18]	5 [7]	.	7 [7]	8 [7]	.	8 [14]	.	10 [14]	8 [15]	13 [14]	40 [19]	42 [19]	36 [14]	82 [31]	30 [6]	.
Callitricho-Myriophylletum																	
Callitriche hamulata	23 [22]	.	.	.	.	.	.	.	.	.	.	36 [22]	37 [22]	81 [22]	.	10 [3]	.
Myriophyllum alterniflorum	10 [16]	.	.	.	.	.	.	.	.	.	.	15 [16]	15 [16]	34 [16]	.	.	.
Ranunculus aquatilis agg.	24 [20]	2 [3]	.	.	.	<1 [3]	.	.	.	.	.	36 [20]	37 [20]	82 [20]	.	.	.
Potamogeton alpinus	5 [15]	2 [3]	.	2 [2]	3 [3]	.	2 [3]	.	3 [3]	8 [3]	.	7 [17]	8 [17]	17 [17]	.	.	.
Ranunculo-Sietum																	
Ranunculus trichophyllus	1 [9]	2 [15]	.	2 [15]	3 [15]	.	.	.	.	.	.	1 [7]	1 [7]	.	18 [7]	.	.
Groenlandia densa	1 [38]	.	.	.	.	.	.	.	.	.	.	1 [38]	1 [38]	.	12 [38]	.	.
Zannichellia palustris	4 [25]	.	.	.	.	.	.	.	.	.	.	6 [99]	7 [25]	.	82 [25]	.	.
Hippuris vulgaris	1 [1]	2 [25]	.	2 [1]	3 [1]	.	.	.	.	.	.	1 [1]	1 [1]	.	12 [1]	.	.
Ranunculetum fluitantis																	
Ranunculus fluitans	5 [35]	.	.	.	.	.	.	.	.	.	.	7 [35]	8 [35]	6 [38]	.	100 [33]	.

No. of species / relevé	6.6	6.4	6	5.2	5.2	9.6	6.2	3.5	6.9	7.6	6.7	6.8	6.9	7.2	7.6	5.6	3
No. of relevés	336	59	1	41	40	16	52	2	40	12	24	219	212	95	17	10	1
	Potametea	Potametalia	Potamion graminei	Potamion lucentis	Potametum lucentis	Potamion pusilli	Nymphaeetalia	Hydrocharition	Nymphaeion albae	Myriophyllo-Nupharetum	Sparganio-Elodeetum	Batrachietalia	Ranunculion fluitantis	Callitricho-Myriophylletum	Ranunculo-Sietum	Ranunculetum fluitantis	Phragmitetea
Phragmitetea																	
Typha latifolia	<1 [15]	.	.	.	.	.	.	.	.	.	.	<1 [15]	.	.	.	.	.
Phragmites australis	1 [5]	2 [1]	.	2 [1]	.	.	2 [15]	.	.	.	.	.	.	.	.	.	100 [1]
Sparganium erectum	8 [6]	8 [7]	100 [1]	2 [15]	3 [15]	19 [7]	6 [7]	.	5 [3]	.	8 [3]	9 [6]	9 [6]	2 [38]	24 [3]	.	100 [<1]
Alisma plantago-aquatica	8 [3]	8 [1]	100 [1]	2 [1]	3 [1]	19 [1]	6 [5]	.	8 [5]	.	13 [5]	8 [4]	8 [4]	6 [8]	6 [1]	.	.
Glyceria maxima	6 [13]	7 [21]	.	10 [21]	10 [21]	.	12 [4]	.	10 [6]	8 [3]	13 [7]	5 [15]	5 [15]	3 [18]	.	.	100 [<1]
Rumex hydrolapathum	<1 [15]	.	.	.	.	.	.	.	.	.	.	<1 [15]	.	.	.	.	.
Sium latifolium	1 [14]	.	.	.	.	.	4 [9]	.	5 [9]	.	8 [9]	1 [20]	1 [20]	1 [3]	.	.	.
Schoenoplectus lacustris	1 [2]	.	.	.	.	.	.	.	.	.	.	2 [56]	1 [2]	.	.	10 [3]	.
Butomus umbellatus	13 [8]	19 [8]	.	10 [5]	8 [7]	44 [9]	12 [14]	.	3 [1]	.	.	11 [6]	11 [7]	1 [3]	.	10 [3]	.
Mentha aquatica	6 [6]	.	.	.	.	.	.	.	.	.	.	9 [6]	9 [6]	9 [1]	35 [3]	.	.
Veronica beccabunga	6 [3]	2 [15]	.	2 [15]	3 [15]	.	.	.	.	.	.	9 [3]	9 [3]	1 [15]	76 [2]	.	.
Veronica anagallis-aquatica	8 [7]	.	.	.	.	.	.	.	.	.	.	12 [7]	12 [7]	8 [8]	76 [7]	.	.
Nasturtium officinale	1 [5]	.	.	.	.	.	.	.	.	.	.	2 [5]	2 [5]	.	18 [2]	.	.
Glyceria notata (*G.plicata*)	<1 [1]	.	.	.	.	.	.	.	.	.	.	<1 [1]	.	1 [1]	.	.	.
Phalaris arundinacea	2 [9]	2 [15]	.	2 [15]	3 [15]	.	4 [15]	.	5 [15]	.	8 [15]	2 [5]	2 [5]	1 [<1]	.	.	.
Carex acutiformis	<1 [1]	2 [1]	.	2 [1]	3 [1]	.	.	.	.	.	.	.	.	.	.	.	.
Fontinalietea																	
Platyhypnidium riparioides M	4 [2]	2 [1]	.	2 [1]	3 [1]	.	.	.	.	.	.	5 [2]	6 [2]	.	59 [1]	.	.
Amblystegium riparium M	6 [4]	.	.	.	.	.	.	.	.	.	.	9 [4]	9 [4]	17 [4]	.	.	.
Chiloscyphus polyanthos M	1 [26]	.	.	.	.	.	.	.	.	.	.	2 [26]	2 [26]	5 [26]	.	.	.
Accompanying species																	
Apium inundatum	<1 [3]	.	.	.	.	.	.	.	.	.	.	<1 [3]	.	1 [3]	.	.	.
Callitriche hermaphroditica	1 [6]	3 [3]	.	5 [3]	5 [3]	.	.	.	.	.	.	<1 [3]	.	.	.	.	.
Isolepis fluitans	1 [21]	3 [15]	.	2 [15]	3 [15]	6 [15]	2 [38]	.	3 [38]	.	4 [38]	<1 [15]	.	1 [15]	.	.	.
Luronium natans	<1 [38]	2 [38]	100 [38]	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton filiformis	1 [8]	2 [1]	.	2 [1]	3 [1]	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton polygonifolius	1 [39]	.	.	.	.	.	.	.	.	.	.	1 [39]	1 [39]	1 [15]	.	.	.
Utricularia australis	<1 [15]	.	.	.	.	.	2 [15]	.	3 [15]	8 [15]	.	.	.	.	.	.	.

Table 4.1b Macrophyte vegetation of north-west German running waters in 2010/2011 as classified after Preising et al. (1990). Relevés assigned to lower levels than the class belong to several groups; 332 relevés are included. No specific character species is attributed to the Nymphaeion albae, which is characterized by differential species. Base figures: relative frequency of species occurrence within a group in percent; exponents: cover values as averages within groups

No. of species / relevé	3.7	6.9	7	7.6	8.1	7.1	7.7	8.1	7.4	8.4	6.5	6.6	7.4	6.2	6.1	1.4	2
No. of relevés	18	305	25	11	9	10	92	75	11	44	183	171	65	9	7	7	2
	Lem-netea	Pota-metea	Pota-meta-lia	Pota-mion lucen-tis	Pota-metum lucen-tis	Pota-mion pusilli	Nym-phae-etalia	Nym-phae-ion albae	Myrio-phyllo-Nuphar-etum	Spar-ganio-Elode-etum	Batra-chieta-lia	Ranun-culion fluitan-tis	Callitri-cho-My-riophyll-etum	Ranun-culo-Sietum	Ranun-culetum fluitantis	Phrag-mite-tea	Fonti-nalie-tea
Lemnetea																	
Spirodela polyrhiza	72 $^{<1}$	38 ^{2}	68 ^{1}	82 ^{1}	100 ^{1}	70 ^{1}	63 ^{4}	64 ^{4}	73 ^{18}	61 ^{1}	20 ^{1}	20 ^{1}	18 ^{1}	.	14 $^{<1}$	.	.
Lemna minor	100 ^{2}	67 ^{1}	88 ^{1}	100 ^{2}	100 ^{1}	90 ^{1}	88 ^{2}	93 ^{2}	91 ^{8}	95 ^{1}	53 ^{1}	52 ^{1}	55 ^{1}	33 $^{<1}$	29 $^{<1}$	.	.
Wolffia arrhiza	6 $^{<1}$	<1 $^{<1}$	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lemna trisulca	22 ^{9}	12 $^{<1}$	8 $^{<1}$	18 $^{<1}$	22 $^{<1}$	.	24 $^{<1}$	25 $^{<1}$	27 ^{1}	34 $^{<1}$	6 $^{<1}$	6 $^{<1}$	6 $^{<1}$	.	14 $^{<1}$	.	.
Lemna gibba	6 $^{<1}$	10 ^{1}	24 ^{2}	27 ^{2}	33 ^{2}	30 ^{1}	16 ^{1}	17 ^{1}	27 ^{3}	14 ^{1}	6 $^{<1}$	6 $^{<1}$	5 ^{1}	.	.	.	.
Potametea																	
Elodea canadensis	.	27 ^{4}	16 ^{5}	18 ^{1}	22 ^{1}	20 ^{9}	25 ^{2}	27 ^{2}	9 ^{1}	41 ^{1}	28 ^{5}	27 ^{6}	35 ^{2}	.	100 ^{9}	.	.
Potamogeton natans	.	13 ^{13}	16 ^{5}	9 ^{1}	11 ^{1}	30 ^{6}	20 ^{16}	21 ^{16}	.	30 ^{17}	9 ^{12}	10 ^{12}	11 ^{9}	.	.	.	.
Potamogeton crispus	.	9 ^{3}	8 ^{9}	9 ^{3}	11 ^{3}	.	4 ^{4}	5 ^{4}	9 $^{<1}$	2 ^{1}	12 ^{2}	12 ^{2}	11 ^{3}	33 $^{<1}$	14 ^{1}	.	.
Ceratophyllum demersum	.	8 ^{4}	16 ^{4}	18 ^{8}	22 ^{8}	20 $^{<1}$	17 ^{4}	19 ^{5}	.	20 ^{7}	3 ^{1}	3 ^{1}	3 ^{1}	.	.	.	.
Persicaria amphibia	.	5 ^{1}	16 ^{1}	9 ^{1}	11 ^{1}	20 ^{2}	7 ^{1}	5 $^{<1}$	.	5 ^{1}	3 $^{<1}$	3 $^{<1}$	2 $^{<1}$	.	.	.	.
Potametalia																	
Potamogeton acutifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton berchtoldii	.	<1 ^{3}	.	.	.	.	1 ^{3}	1 ^{3}	.	2 ^{3}	.	.	.	.	.	.	.
Potamogeton compressus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton pectinatus	.	12 ^{12}	32 ^{10}	36 ^{5}	22 ^{3}	.	16 ^{18}	20 ^{8}	.	7 ^{2}	8 ^{3}	8 ^{18}	3 ^{3}	11 ^{15}	.	.	.
Potamion lucentis																	
Myriophyllum spicatum	.	8 ^{4}	8 ^{4}	18 ^{4}	.	.	11 ^{6}	9 ^{8}	36 ^{13}	5 $^{<1}$	6 ^{4}	6 ^{4}	5 ^{3}	33 ^{3}	.	.	.
Ranunculus circinatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potametum lucentis																	
Potamogeton lucens	.	4 ^{18}	16 ^{48}	36 ^{48}	44 ^{48}	.	5 ^{7}	7 ^{7}	9 ^{15}	9 ^{5}	2 ^{2}	2 ^{2}	5 ^{2}	.	.	.	.
Potamogeton perfoliatus	.	4 ^{7}	24 ^{12}	45 ^{14}	56 ^{14}	10 $^{<1}$	2 ^{2}	3 ^{2}	.	5 ^{2}	2 ^{2}	2 ^{2}	3 ^{2}	.	.	.	.
Potamion pusilli																	
Potamogeton pusillus	.	4 ^{8}	12 ^{18}	.	.	30 ^{18}	4 ^{5}	4 ^{6}	.	2 ^{15}	3 ^{4}	3 ^{4}	3 ^{8}	.	.	.	.
Elodea nuttallii	.	25 ^{9}	56 ^{24}	36 ^{5}	44 ^{5}	100 ^{32}	36 ^{5}	41 ^{5}	45 ^{7}	45 ^{4}	16 ^{6}	17 ^{6}	17 ^{6}	11 ^{1}	29 ^{8}	.	.
Potamogeton trichoides	.	<1 $^{<1}$	.	.	.	.	1 $^{<1}$	1 $^{<1}$	.	2 $^{<1}$	.	.	.	.	.	.	.

No. of species / relevé	3.7	6.9	7	7.6	8.1	7.1	7.7	8.1	7.4	8.4	6.5	6.6	7.4	6.2	6.1	1.4	2
No. of relevés	18	305	25	11	9	10	92	75	11	44	183	171	65	9	7	7	2
	Lem-netea	Pota-metea	Pota-meta-lia	Pota-mion lucen-tis	Pota-metum lucen-tis	Pota-mion pusilli	Nym-phae-etalia	Nym-phae-ion albae	Myrio-phyllo-Nuphar-etum	Spar-ganio-Elode-etum	Batra-chieta-lia	Ranun-culion fluitan-tis	Callitri-cho-My-riophyll-etum	Ranun-culo-Sietum	Ranun-culetum fluitantis	Phrag-mite-tea	Fonti-nalie-tea
Nymphaeetalia																	
Myriophyllum verticillatum	.	<1 [1]	.	.	.	.	.	.	.	.	11	1 [1]	2 [1]	.	.	.	.
Utricularia vulgaris	.	3 [5]	.	.	.	.	10 [5]	11 [6]	27 [8]	2 [5]	1 [3]	1 [3]	.	.	.	.	.
Hydrocharition																	
Hydrocharis morsus-ranae	.	4 [2]	12 [1]	18 [1]	22 [1]	10 [<1]	9 [2]	8 [3]	9 [15]	5 [<1]	1 [2]	1 [2]	.	.	.	.	.
Myriophyllo-Nupharetum																	
Nuphar lutea	.	33 [11]	20 [15]	36 [15]	44 [15]	10 [15]	77 [12]	77 [13]	82 [32]	77 [11]	13 [6]	14 [6]	9 [4]	.	.	.	.
Sparganio-Elodeetum																	
Sagittaria sagittifolia	.	29 [12]	36 [21]	45 [25]	56 [25]	40 [17]	70 [12]	83 [12]	45 [13]	98 [14]	9 [8]	10 [8]	8 [12]	.	.	.	.
Sparganium emersum	.	64 [8]	52 [8]	55 [8]	44 [7]	40 [9]	51 [6]	52 [6]	36 [14]	52 [5]	74 [9]	77 [9]	92 [8]	22 [2]	86 [5]	.	.
Batrachietalia																	
Callitriche palustris agg.	.	44 [2]	24 [1]	9 [3]	11 [3]	50 [1]	35 [1]	43 [1]	27 [<1]	50 [1]	52 [3]	53 [3]	72 [4]	44 [4]	57 [1]	.	.
Glyceria fluitans	.	8 [4]	.	.	.	.	2 [3]	3 [3]	.	5 [3]	12 [4]	9 [5]	15 [2]	.	.	.	.
Agrostis stolonifera	33 [<1]	15 [<1]	4 [1]	9 [1]	11 [1]	.	4 [<1]	4 [<1]	27 [<1]	.	22 [1]	21 [<1]	9 [1]	22 [<1]	.	.	.
Ranunculion fluitantis																	
Fontinalis antipyretica M	.	6 [4]	.	.	.	.	.	.	.	.	10 [4]	11 [4]	12 [1]	33 [<1]	29 [1]	.	50 [<1]
Potamogeton nodosus	.	1 [4]	.	.	.	.	1 [3]	1 [3]	.	2 [3]	1 [5]	1 [5]	2 [5]	.	.	.	.
Berula erecta	.	23 [6]	.	.	.	.	3 [1]	4 [1]	9 [1]	5 [2]	36 [6]	38 [6]	28 [4]	22 [46]	.	.	.
Callitricho-Myriophylletum																	
Callitriche hamulata	.	16 [2]	.	.	.	.	3 [<1]	4 [<1]	9 [<1]	5 [1]	26 [2]	27 [2]	66 [2]	11 [3]	29 [<1]	.	.
Myriophyllum alterniflorum	.	6 [2]	.	.	.	.	.	.	.	.	10 [2]	10 [2]	26 [3]	.	14 [<1]	.	.
Ranunculus aquatilis agg.	.	10 [7]	.	.	.	.	.	.	.	.	17 [7]	19 [7]	49 [7]	.	.	.	.
Ranunculo-Sietum																	
Ranunculus trichophyllus	.	2 [4]	.	.	.	.	.	.	.	.	4 [4]	4 [4]	2 [<1]	67 [4]	.	.	.
Groenlandia densa	.	<1 [1]	.	.	.	.	.	.	.	.	1 [1]	1 [1]	.	11 [1]	.	.	.
Zannichellia palustris	.	1 [1]	.	.	.	.	.	.	.	.	21	2 [1]	.	22 [1]	.	.	.
Ranunculetum fluitantis																	
Ranunculus fluitans	.	3 [12]	.	.	.	.	.	.	.	.	4 [12]	5 [12]	2 [3]	.	100 [13]	.	.

No. of species / relevé	3.7	6.9	7	7.6	8.1	7.1	7.7	8.1	7.4	8.4	6.5	6.6	7.4	6.2	6.1	1.4	2
No. of relevés	18	305	25	11	9	10	92	75	11	44	183	171	65	9	7	7	2
	Lem-netea	Pota-metea	Pota-meta-lia	Pota-mion lucen-tis	Pota-metum lucen-tis	Pota-mion pusilli	Nym-phae-etalia	Nym-phae-ion albae	Myrio-phyllo-Nuphar-etum	Spar-ganio-Elode-etum	Batra-chieta-lia	Ranun-culion fluitan-tis	Callitri-cho-My-riophyll-etum	Ranun-culo-Sietum	Ranun-culetum fluitantis	Phrag-mite-tea	Fonti-nalie-tea
Phragmitetea																	
Iris pseudacorus	6 <1	2 1	.	.	.	.	.	.	.	.	4 1	4 1	3 <1	11 1	.	.	.
Phragmites australis	33 10	9 5	16 4	9 15	11 15	20 1	10 2	5 2	.	2 1	7 8	7 8	3 2	.	.	43 9	.
Sparganium erectum	33 26	32 5	20 10	9 15	.	10 15	43 5	45 4	55 8	45 3	27 5	26 5	22 2	.	.	.	.
Alisma plantago-aquatica	.	3 1	4 <1	.	.	10 <1	4 <1	5 <1	.	7 <1	3 1	3 1	3 3	.	14 1	.	.
Glyceria maxima	17 10	17 3	20 3	18 3	22 3	30 3	25 4	24 4	18 8	23 4	13 2	13 2	15 2	.	14 3	14 <1	.
Rumex hydrolapathum	.	3 <1	.	.	.	.	5 <1	7 <1	9 1	5 <1	2 1	1 1	2 1	.	.	.	.
Sium latifolium	.	1 5	.	.	.	.	.	.	.	.	2 5	2 5	2 15	.	.	.	.
Schoenoplectus lacustris	.	1 1	.	.	.	.	111	1 1	9 1	.	133	1 2	.	.	.	.	.
Butomus umbellatus	.	13 3	8 9	9 15	11 15	10 3	18 3	19 3	9 1	18 5	11 3	12 3	3 9	.	.	.	.
Mentha aquatica	6 5	6 3	.	.	.	.	.	.	.	.	9 3	9 4	9 1	11 38	.	14 1	.
Veronica beccabunga	.	6 1	.	.	.	.	1 1	1 1	.	2 1	9 1	9 1	9 1	44 <1	14 <1	14 1	.
Veronica anagallis-aquatica	.	3 <1	.	.	.	.	2 <1	1 <1	.	2 <1	4 <1	4 <1	3 <1	44 <1	.	.	.
Mimulus guttatus	.	1 2	.	.	.	.	.	.	.	.	1 2	.	.	.	.	.	.
Nasturtium officinale	.	7 7	.	.	.	.	2 <1	.	.	.	11 8	12 8	14 3	22 44	.	.	.
Phalaris arundinacea	28 4	58 2	68 2	82 1	78 1	60 2	48 3	48 3	36 5	52 3	61 2	61 2	66 2	89 1	57 <1	14 3	.
Carex acutiformis	.	<1 <1	.	.	.	.	.	.	.	.	1 <1	1 <1	.	.	.	.	.
Carex riparia	6 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	29 <1	.
Fontinalietea																	
Platyhypnidium riparioides M	.	4 5	4 1	.	.	.	.	.	.	.	7 6	6 6	5 <1	22 1	.	14 15	50 75
Chiloscyphus polyanthos M	.	1 4	.	.	.	.	.	.	.	.	2 4	2 4	2 <1	.	.	.	100 1
Accompanying species																	
Callitriche hermaphroditica	61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Isolepis fluitans	.	<1 1	.	.	.	.	.	.	.	.	1 1	1 1	2 1	.	.	.	.
Potamogeton praelongus	.	1 3	.	.	.	.	1 3	1 3	.	2 3	1 3	1 3	.	.	.	.	.

Table 4.5 Correlation coefficients after Spearman and p values of the relationships between environmental variables and DCA axes 1 and 2 for a total of 650 relevés that were used for the trajectory analysis

Parameter	r DCA axis 1	p	r DCA axis 2	p
Current velocity	0.13	***<0.001	0.23	***<0.001
Reach width	-0.30	***<0.001	-0.16	***<0.001
Reach depth	-0.35	***<0.001	-0.07	0.058
EIV - temperature	-0.29	***<0.001	0.04	0.330
EIV - soil reaction	-0.04	0.270	0.16	***<0.001
EIV - nutrients	-0.21	***<0.001	0.07	0.085

Table 4.7 Correlation coefficients after Spearman and p values of the relationships between environmental variables and DCA axes 1 and 2 for 70 streams or rivers (1950s and 2010/2011)

Parameter	r DCA axis 1	p	r DCA axis 2	p
Current velocity	0.49	***<0.001	0.16	0.095
Reach width	-0.21	*0.026	0.21	*0.028
Reach depth	-0.41	***<0.001	0.15	0.118
EIV - temperature	-0.58	***<0.001	0.24	**0.004
EIV - soil reaction	-0.16	0.053	-0.18	*0.033
EIV - nutrients	-0.27	***<0.001	-0.22	*0.010

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